Limited attention diminishes spatial suppression from large field Glass patterns

Andrea Pavan[1,*], Adriano Contillo[2], Filippo Ghin[1], Matthew J. Foxwell[1] and George Mather[1]

[1]University of Lincoln, School of Psychology, Brayford Wharf East, Lincoln LN5 7AY, United Kingdom

[2]University of Ferrara, Department of Physics and Earth Sciences, Via Saragat 1 44122, Ferrara, Italy

***Corresponding Author**

Andrea Pavan

University of Lincoln

Brayford Wharf East

Lincoln LN5 7AY

United Kingdom

Email: apavan@lincoln.ac.uk

Telephone: +44(0)1522 88 6154

Abstract

Glass patterns (GPs) consist of randomly distributed dot pairs (dipoles) whose orientations are determined by specific geometric transforms. We investigated the role of visuospatial attention in the processing of global form from GPs by measuring the effect of distraction on adaptation to GPs. In the non-distracted condition, observers were adapted to coherent GPs. After the adaptation period, they were presented with a test GP divided in two halves along the vertical and were required to judge which side of the test GP was more coherent. In the attention-distracted condition, a high-load rapid serial visual presentation task was performed during the adapting period. The magnitude of the form after-effect was measured using a technique that measures the coherence level at which the test GP appears random. The rationale was that if attention has a modulatory effect on the spatial summation of dipoles, in the attention-distracted condition we should expect a weaker form after-effect. However, the results showed stronger form after-effect in the attention-distracted condition than in the non-distracted condition, suggesting that distraction during adaptation increases the strength of form adaptation. Additional experiments suggested that distraction may reduce the spatial suppression from large-scale textures, strengthening the spatial summation of local-oriented signals.

Keywords: Glass patterns, form adaptation, form after-effect, visuospatial attention, spatial suppression

Introduction

Glass patterns (GPs) (Glass, 1969) are textures formed by multiple dot pairs (dipoles), spatially arranged according to specific geometric transformations in order to create different configurations (Glass & Pérez, 1973; Glass & Switkes, 1976). GPs are commonly used to investigate the pooling of local and correlated orientation signals into a global percept of form (Clifford & Weston, 2005; Dakin, 1997; Dakin & Bex, 2002; Lin, Cho, & Chen, 2017; Pavan, Hocketstaller, Contillo, & Greenlee, 2016; Wilson & Wilkinson, 1998, 2003; Wilson, Switkes, & De Valois, 2004; Wilson, Wilkinson, & Asaad, 1997). There is physiological evidence in macaque monkeys that simple and complex cells in visual areas V1 and V2 show orientation selectivity for static oriented GPs presented in their classical receptive field (Smith, Bair, & Movshon, 2002; Smith, Kohn, & Movshon, 2007). There is corresponding evidence from human brain imaging that early visual areas play an important role in representing local orientation structure for the perception of complex spatial form (Mannion, McDonald, & Clifford, 2009, 2010; Ostwald, Lam, Li, & Kourtzi, 2008; Swettenham, Anderson, & Thai, 2010).

However, evidence is scarce on the role of visuospatial attention in the spatial summation of local oriented cues to extract global form from GPs. Attention modulates early processing of visual information (Ling, Pratte, & Tong, 2015; T. Liu, Larsson, & Carrasco, 2007; McAdams & Maunsell, 1999a, 1999b; Motter, 1993; Poltoratski, Ling, McCormack, & Tong, 2017; Somers, Dale, Seiffert, & Tootell, 1999; Treue & Martinez-Trujillo, 2007) by enhancing the encoding of task-relevant visual information (Cohen & Tong, 2015; Jehee, Brady, & Tong, 2011), de-noising visual information at low levels of visual processing and subsequently amplifying the signal at higher stages of visual processing (Pratte, Ling, Swisher, & Tong, 2013). It has been demonstrated that attention is involved in the integration of visual information occupying distant parts of the visual field (Haynes, Tregellas, & Rees, 2005). Haynes et al. (2005), using functional MRI, found that a task requiring the integration of information between two attended but spatially separated stimuli, modulated the degree of connectivity (functional integration) between their (retinotopic) representations in early visual areas. Therefore, visuospatial attention may bind together cortical sites at multiple levels of the visual hierarchy that are commonly involved in processing attended stimuli, thus promoting the integration between functionally isolated cortical sites (Haynes et al., 2005). These results are in line with recent neurophysiological findings of Ruff and Cohen (2016), who showed that visual attention improves stimulus encoding within a specific cortical area and affects the extent to which visual information is transmitted between cortical areas.

Dickinson et al. (2009), using large-scale GPs, found that the size and topology of the area of attentional integration of local orientation cues is not fixed, but the spatial extent of integration is flexibly adjusted; attentional integration can occur over large distances (over 10 deg in radius) and can be constrained to both circular and annular apertures. These results suggest that the aperture can be attentively modulated and visual integration in the selected areas can be optimized through the exclusion of noise outside the regions of interest. Palomares et al. (2012) investigated local and global processing of GPs using a combination of fMRI and steady-state visual evoked potentials (SSVEP). In order to compare the activity associated with local and global processing, they examined two frequency components of the SSVEP in each considered visual area: the high temporal frequency at which dipole position was updated (30 Hz) and the low temporal frequency at which the global pattern was updated (.83 Hz). Additionally, in order to assess the role of sustained attention in processing local and global activity, responses were measured either directing attention toward the stimulus or diverting it away using a rapid serial visual presentation task. Modulatory effects of attention were observed for the global responses to GPs in a series of early visual areas including V1, V3A, V4, LOC and hMT+, but not for the local responses from the same areas. However, when attention was diverted away from stimulus coherence, both local and global responses were lower. These results point to the role of attention in modulating the activity of early visual areas in response to the local and global structure of GPs.

On the basis of these behavioural and brain imaging studies, it can be argued that visuospatial attention plays an important role in encoding and pooling sparse local orientation cues into global form. However, other behavioural studies support the notion that attention may not be involved in the extraction of global form. Chung and Khuu (2014) investigated the role of awareness in the perception of radial and spiral GPs using a continuous flash suppression (CFS) paradigm to suppress visual awareness (Maruya, Watanabe, & Watanabe, 2008; Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006). The authors found that the lack of awareness had no effect on the processing and integration of global form and motion from circular and radial GPs. These results suggest that mechanisms responsible for the perception of GPs do not require conscious attentional modulation. Dakin and Bex (2001) investigated the spatial (local and global) frequency tuning of the grouping process for perception of GPs. They reported that the tuning of local grouping is band-pass, being selective to a narrow range of spatial frequencies, whereas the tuning of global grouping is broad and low-pass, i.e., dipoles are pooled across a broad range of low spatial frequencies. However, Dakin and Bex (2001) found no evident influence of attention and top-down factors on the spatial tuning of the pooling process. Using an adaptation paradigm, Pavan et al. (2016) have demonstrated that adapting to oriented GPs induces a weak form of tilt after-effect (TAE) and that its magnitude depends on attention. They also assessed whether the distraction-induced reduction of the TAE was mediated by the spatial summation of local orientation signals or adaptation to the global orientation of GPs. Results showed no evidence of attentional effects on the extraction of global form from translational GPs.

In this study, we further investigated the role of visuospatial attention in form perception from GPs by investigating the effect of attention during adaptation on coherence thresholds in GPs. Adaptation to either static or dynamic GPs produces an increment of coherence thresholds (a higher level of coherence is required for distinguishing coherent from random patterns), consistent with adaptation-induced suppression of the spatial summation of local dipoles during extraction of global form (Clifford & Weston, 2005; Ross & Dickinson, 2007; Vreven & Berge, 2007). In the present study participants' attention was diverted away from the adapting GP pattern using a concomitant rapid serial visual presentation task (RSVP) (Kaunitz, Fracasso, & Melcher, 2011; Pavan & Greenlee, 2015; Pavan et al., 2016). After the adaptation period, participants were presented with a test GP divided in two halves along the vertical and were required to judge which side of the test GP was more coherent. The strength of the form after-effect was estimated by measuring the null point at which the GP just appeared random (coherence level at which participants were at chance in discriminating the most coherent side; point of subjective randomness or PSR).

On the basis of Dickinson et al. (2009) and Palomares et al. (2012), it was predicted that if form perception from GPs requires visuospatial attention to pool the local and sparse orientation signals from dipoles, then diverting the attention away from the adapting GP will induce a weaker form after-effect (smaller adaptation-induced rise in coherence at the PSR relative to the non-distracted adaptation condition).

To anticipate, the results showed that diverting the attention away from the adapting GP produced a *larger* adaptation-induced rise in PSR values (stronger form after-effect) relative to the non-distracted condition. In order to seek an explanation for this counterintuitive result, in a series of additional experiments we manipulated the spatial and temporal characteristics of GPs. The results are compatible with the notion that limited attentional resources may reduce the suppression of neurons integrating local signals from large-scale textures, thus enhancing global form perception.

Experiment 1

In Experiment 1 we investigated the role of attention in the processing of global form from Glass patterns (GPs) by using a high-load secondary task during form adaptation to static GPs. The rationale was that if attention has a modulatory effect on the spatial integration of local oriented cues (dipoles) to extract global form from GPs, then diverting attention away from the adapting pattern should produce a weaker form after-effect than in the non-distracted condition.

Methods

Participants

Two of the authors (FG and MF) and seven naïve participants took part voluntarily in the experiment. All participants had normal or corrected to normal visual acuity. Viewing was binocular. Methods conformed to the World Medical Association Declaration of Helsinki (2013). This study was approved by the Ethics Committee of the University of Lincoln. Written informed consent was obtained from each participant prior to enrolment in the study.

Apparatus

Stimuli were displayed on a 20-inch HP p1230 monitor with a refresh rate of 85 Hz. Stimuli were generated with Matlab PsychToolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1280 x 1024 pixels. Each pixel subtended approximately .0315 deg (i.e.,~1.9 arc min). The minimum and maximum luminances of the screen were .08 and 74.6 cd/m^2 respectively, and the mean luminance was 37.5 cd/m^2. A digital-to-analogue converter (Bits#

V2.0, Cambridge Research Systems, Cambridge UK) was used to increase the dynamic contrast range (13-bit luminance resolution). A 13-bit gamma-corrected lookup table (LUT) was applied so that luminance was a linear function of the digital representation of the image.

Stimuli

Static translational Glass patterns (GPs) were used (Figure 1A). Each GP consisted of 2000 dipoles, with each dot having a width of .04 deg, and an inter-dot spacing of .18 deg (Clifford & Weston, 2005). The Weber contrast of each dot was .99. The GPs were displayed within an annulus with an outer radius of 7.25 deg and an inner radius of .85 deg. The density was 12.3 dipoles/deg^2.

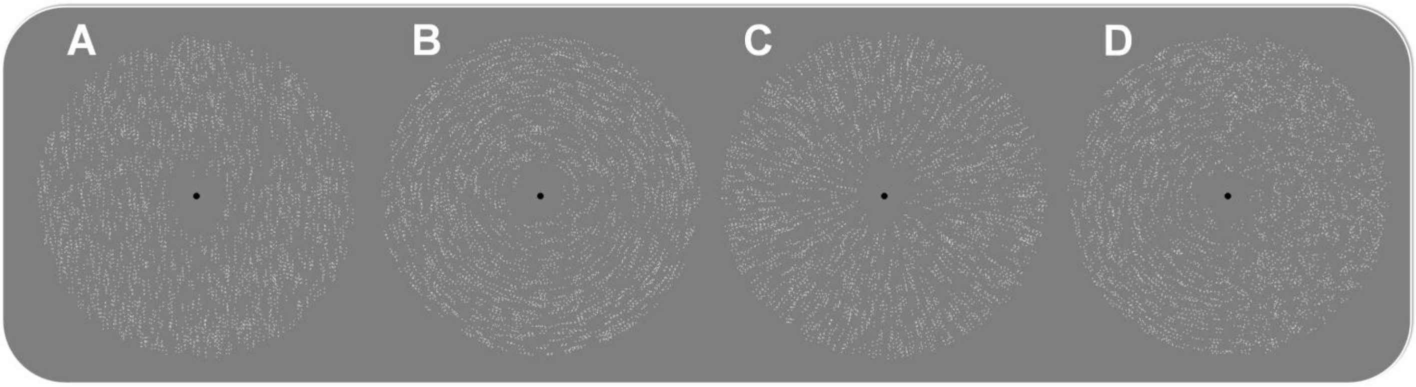

Figure 1. Stimuli used in Experiment 1. The Glass patterns (GP) represented have 100% coherence. (A) Translational GP, (B) Circular GP, (C) Radial GP, (D) Test GP; one half is 100% coherent (left side) whereas the other half (right side) is composed of randomly oriented dipoles (only a circular test GP is shown).

Procedure

Participants took part in three conditions for each GP configuration (Figure 2). First, they completed a baseline condition (i.e., no-adaptation condition), after which they completed the adaptation and distraction conditions. The order in which they completed the latter two conditions was randomised across participants.

Condition 1: no adaptation (baseline)

Participants were seated 57 cm in front of the computer screen and asked to place their head on a head rest for the duration of the experiment, and maintain fixation on a central marker. The room was darkened. Participants first completed a baseline condition, in which they were asked to judge which side of a vertically divided GP had the highest level of coherence. For each divided GP shown, the side which displayed the coherent GP was randomised on a trial by trial basis (two-alternative forced choice task; 2AFC). Each side of the divided GP contained 1000 dipoles. In order to avoid abrupt stimulus onset, the GP was presented for .5 s within a raised-cosine temporal envelope with .36 s at maximum contrast and .07 s for each ramping on and off (Clifford & Weston, 2005). A 1-up / 1-down staircase (Levitt, 1971) was used to manipulate the number of coherently oriented dipoles displayed on the coherent side of the GP. The step size of the staircase started at 40 (4%) and decreased by 30, 20, 10, 5, 2 and 1 in subsequent reversals. Observers completed the baseline condition (i.e., no-adaptation condition) twice for each GP type (i.e., two 1-up / 1-down staircases). The staircases were terminated either after 300 trials or 20 reversals and converged on the individual point of subjective randomness (PSR), defined as the coherence of the GP for which it became subjectively random. We calculated a PSR for each staircase by averaging the last 12 reversals. The final PSR was obtained by averaging the PSR values calculated from each staircase. One participant (CS) completed one staircase in this condition, but only for translational GPs.

Condition 2: non-distracted

In the non-distracted adaptation condition, participants were presented with an adapting pattern containing a 100% coherent GP, then they judged which half of a divided test GP displayed higher coherence. The structure of the adapting and test GPs was always the same. The initial adapting period lasted for 30 s, followed by a .012 s blank interval, and then the divided test GP was presented for .5 s. After the initial adapting period, a top-up adaptation of 10 s was used (Figure 2B). A new arrangement of dipole locations was generated for both adaptation and test GPs on a trial by trial basis. In order to establish a starting coherence in the test GP, the PSR estimated in the baseline (no adaptation) condition was multiplied by a coefficient so that the initial coherence of the test GP was the closest it could be to 90%, but without exceeding that value. In the non-distracted adaptation condition participants performed one 1-up / 1-down staircase, and it was terminated either after 300 trials or 16 reversals. The PSR was estimated by averaging the last 10 reversals. One participant (CS) performed two staircases in this condition but only for radial GPs; the PSR values estimated from the two staircases were then averaged.

Condition 3: distracted

During the distraction condition, participants completed a rapid serial visual presentation task (RSVP). During the adaptation period, a stream of digits and letters was presented inside the inner circle of the annulus at the same location as the fixation marker in other conditions (Figure 2C). Letters and digits appeared for .25 s interleaved with .15 s of blank screen. The presentation rate was 2.5 Hz with 1 digit every 3 letters (i.e., high-load attentional task; Kaunitz et al., 2011; Pavan et al., 2015, 2016). Letters and digits were randomly presented but two consecutive digits were never presented. Participants were instructed to indicate as fast as possible whether the digit displayed was above or below 5, by pressing either the right arrow key (if the number was above 5) or the left arrow key (if it was lower than 5). Participants had .5 s to respond to the digits. Missed digits were classified as incorrect responses. As in the non-distracted condition, there was an initial adaptation period of 30 s followed by top up adaptation of 10 s. After the adaptation period, the participants judged which side of the divided test GP was more coherent (Figure 2C). In order to prevent responses to numbers of the RSVP sequence immediately before or during the presentation of the test GP, a number could appear in the RSVP sequence no closer than 1.2 s before the test GP. In the distracted adaptation condition participants performed one staircase, and it was terminated either after 300 trials or 16 reversals. The PSR was estimated by averaging the last 10 reversals.

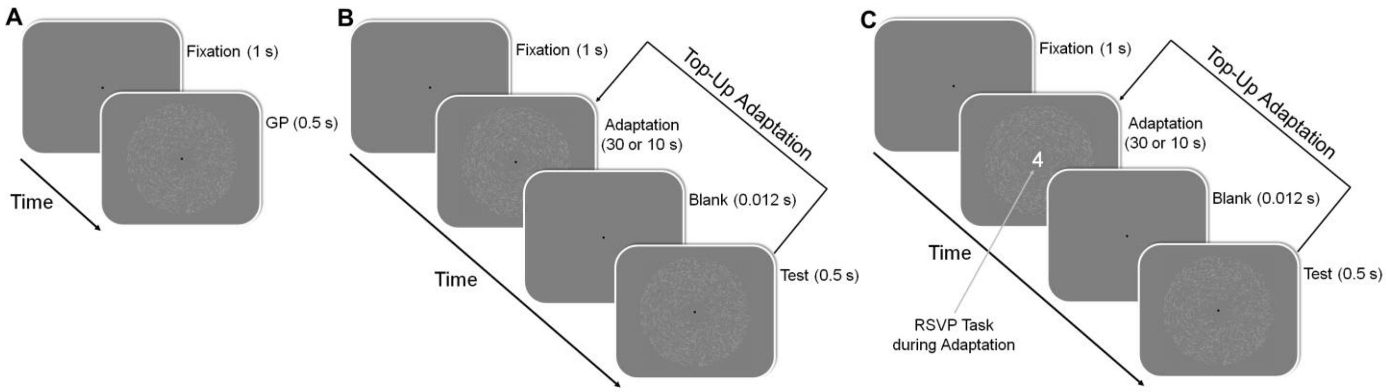

Figure 2. Representation of the conditions used in Experiments 1. (A) Baseline condition. A vertically divided GP is shown with the coherent (100%) side on the left, whereas the right side is composed by randomly oriented dipoles, (B) non-distracted condition, and (C) distracted condition. Only circular GPs are shown, but participants completed also translational and radial GPs. See text for more details about the procedure.

Results

Figure 3 shows the results of Experiment 1. A repeated measures ANOVA including as factors the GP configuration and the adapting condition (no-adaptation, non-distracted and distracted conditions), reported a significant effect of the GP configuration $F(1.24, 9.93) = 12.9$, $p = .0001$, $\eta_p^2 = .617$, and adapting condition $F(2, 16) = 122.13$, $p = .0001$, $\eta_p^2 = .94$. The interaction between GP configuration and adapting condition was not significant $F(4, 32)$

= 0.205, p = .934, η_p^2 = .025. Degrees of freedom were corrected using the Greenhouse-Geisser correction when the sphericity assumption was violated. For the GP configuration, post-hoc comparisons using a False Discovery Rate (FDR; Benjamini & Yekutieli, 1995) with α = .05 reported a significant difference between translational and circular GPs (*adjusted-p* =.013), a significant difference between translational and radial GPs (*adjusted-p* =.0.13) and a significant difference between circular and radial GPs (*adjusted-p* =.013). These results suggest that PSR values estimated for translational GPs were higher than those estimated for circular and radial GPs. In turn, radial GPs produced higher PSR values than circular GPs. These results are in agreement with previous findings of Nankoo et al. (2012) which showed that for static GPs, detection thresholds were lower for circular and radial patterns than vertical or horizontal translational GPs. For the adapting condition, post-hoc comparisons using FDR at .05 reported a significant difference between the no-adaptation condition and both the non-distracted and distracted conditions (both comparisons *adjusted-p* = .0001). Most importantly the post-hoc comparisons also reported a significant difference between the non-distracted and distracted conditions (*adjusted-p* =.004), suggesting higher PSR values in the distracted condition than in the non-distracted adapting condition.

In Figure 3B, individual PSR values estimated in the non-distracted and distracted conditions are reported as a function of the PSR values for the no-adaptation condition. The majority of the points fall above the diagonal line indicating higher PSR for both the non-distracted and distracted conditions. For translational GPs, only 1 point out of 18 fall on the diagonal line indicating equal PSR between the non-distracted and no-adaptation conditions. Similarly, for radial GPs, only 1 point out of 18 fall below the diagonal line indicating higher PSR in the no-adaptation condition than in the non-distracted condition.

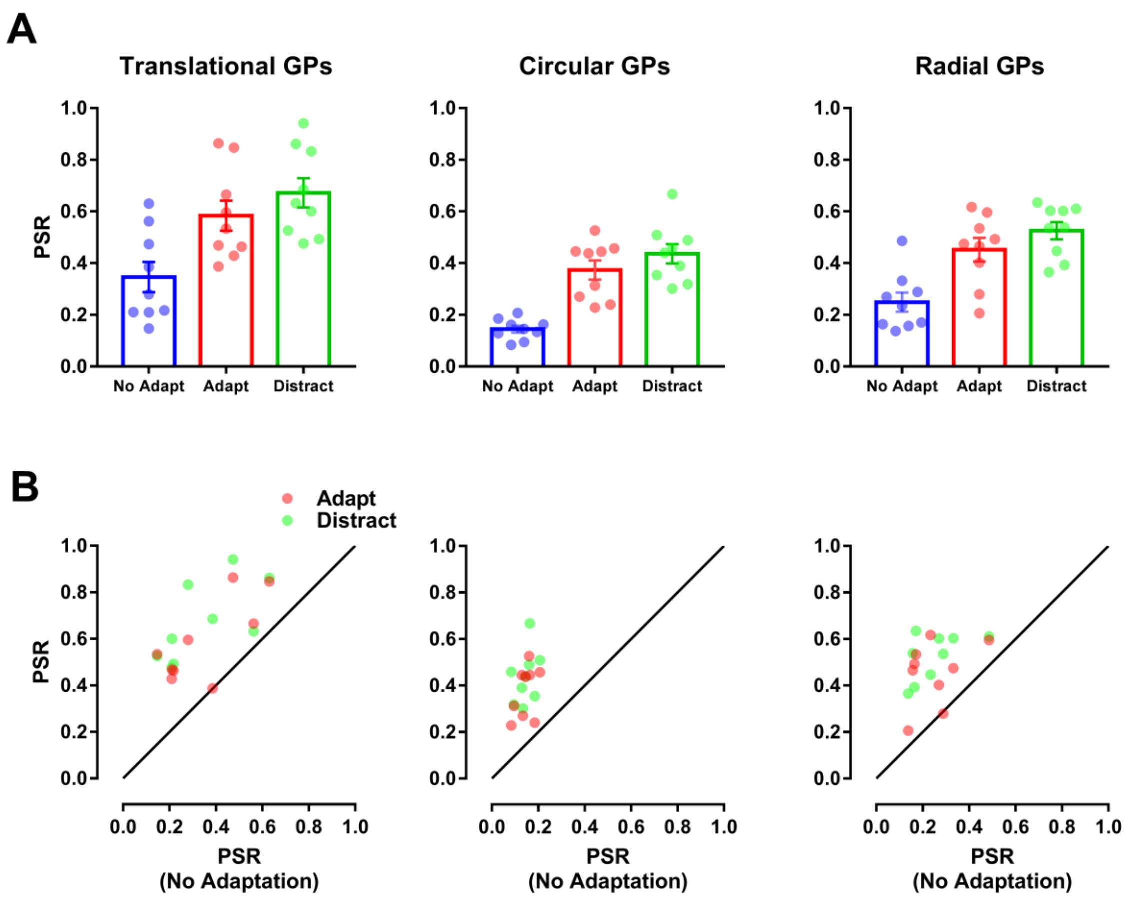

Figure 3. Results of Experiment 1. (A) Mean and individual PSR values for the three GP configurations and for each condition (i.e., no-adaptation, non-distracted, and distracted). PSR values are reported as the proportion of coherent dipoles. (B) Individual PSR values estimated in the non-distracted and distracted conditions as a function of PSR values estimated in the no-adaptation condition for each GP type. The diagonal line indicates equal PSR values for the adaptation (i.e., non-distracted and distracted) and no-adaptation conditions. Error bars ±SEM.

As reported in the methods, the effects of form adaptation from GPs were assessed using a coherence detection task, in which the observers indicated which side of the test GP was more coherent. However, it is worth noting that GP adaptation affects the perceived form of a subsequently presented random test pattern, with the random pattern appearing of a different form (Clifford & Weston, 2005). Therefore, one could ask whether this may introduce a bias in our procedure causing participants' responses to be systematically lower than chance when the coherent side of test GP is at low coherence. This would happen because the random side of the test GP might appear to be more coherent, and the coherent side of the test GP might appear less coherent.

In order to address this possibility, it is necessary to assess whether the asymptotic accuracy of the participants in the limit of vanishing coherence was lower than chance level. Since the 1-up / 1-down staircase is designed to converge on the PSR, such an asymptote may fall outside of the coherence range spanned by the staircase.

In fact, if the asymptote of the underlying psychometric function lies below chance level, the PSR is a pointwise coherence, as depicted in Figure 4A. Consequently, the early steps of the staircase (i.e., the larger steps) will lower the coherence level to some random value in the neighbourhood of the PSR (i.e., either above or below PSR), and the subsequent (smaller) steps will slowly drift the coherence level towards the PSR itself. Therefore, since the psychometric function is symmetrical around the PSR, and the coherence levels after the early steps of the staircase are randomly distributed around the PSR, in turn the late drifts of the staircase will be randomly distributed between the directions of increasing and decreasing coherence levels.

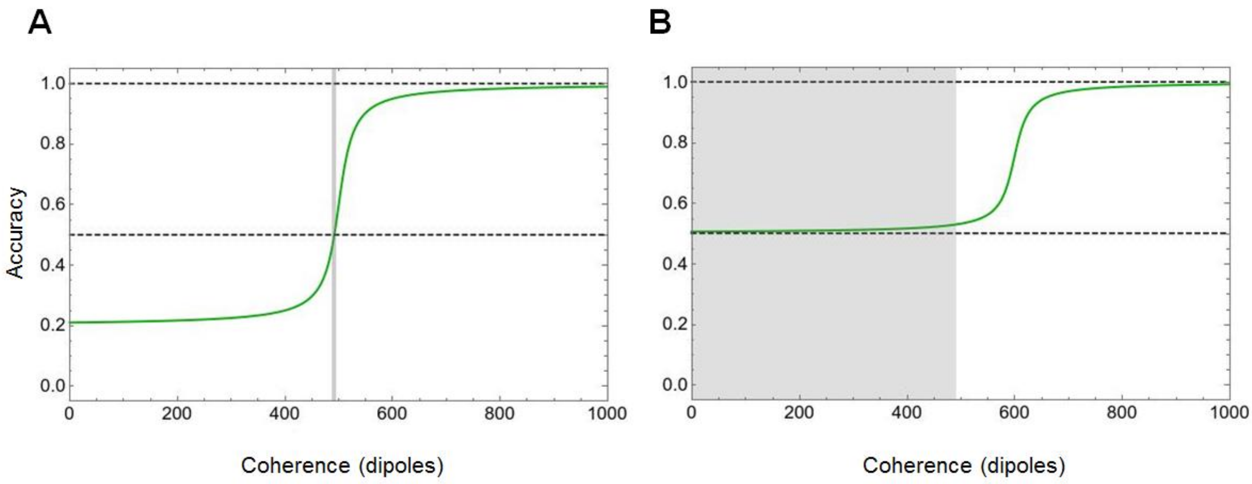

Figure 4. Examples of psychometric functions (solid green curves) with sub-chance (A) and chance (B) lower asymptotes. The dashed lines represent the 100% accuracy and the chance level (50%). The grey areas indicate the location of the PSR: pointwise in the former case (A), widespread in the latter case (B).

The picture completely changes if the lower asymptote coincides with the chance level. In this case, the PSR spreads into a broad range of coherence levels, as depicted in Figure 4B. Since the psychometric function is always very slightly above the chance level, the average rate of correct responses will be slightly higher than the average rate of incorrect responses, therefore, the drift of the late part of the staircase will be skewed towards the direction of decreasing coherence levels. Growing trends of the late drift will therefore become less probable, as a consequence of the high asymmetry of the psychometric function in the asymptotic regime.

A direct consequence of the difference between the two scenarios is that the "late drift" of the staircase can be used as a signature of the actual position of the lower asymptote of the psychometric function, i.e., of the occurrence of a systematic sub-chance response to the test GP. In order to test this, we performed a numerical simulation of the responses to a staircase, by defining a convenient psychometric function:

$$f(c) = \frac{1+\alpha}{2} + \frac{(1-\alpha)\, arctan\big(\beta\,(c-\mu)\big)}{\pi} \qquad \text{Eq. 1}$$

where c is the coherence level of the stimulus, μ represents the midpoint of the function, β encodes the steepness in the midpoint, and α is the value of the lower asymptote (the upper asymptote was set to unity, i.e., 100% accuracy). For the sake of simplicity, we chose to keep constant parameters $\mu = 500$ and $\beta = .1$, and only varied the value of the lower asymptote from $\alpha = .2$ (strongly sub-chance) to $\alpha = .51$ (slightly above the chance level).

The simulation consisted in defining a starting coherence c = 1000 and generating a random number in the interval {0, 1}. If the random number was smaller than the value of the psychometric function corresponding to the selected coherence, the coherence level itself was decreased by a step of 40 (as in the actual implementation of the staircase used in the experiment). Otherwise, the coherence level was increased by an equivalent step. The procedure was iterated for a total of 300 steps, while the size of the steps was decreased at each reversal of the staircase, along the pattern of the actual staircase. At this point, a linear fit was applied to the staircase entries comprised between the 8th and the 20th reversal (i.e., when the step size had already reached its minimum value), and the slope of the resulting line was recorded as a measure of the late drift mentioned above. In order to achieve sufficient statistical power, the staircase was repeated for α varying from .2 to .51 with steps of .005, 10^4 times for each value of α. Mean values and standard deviations of the slope as functions of α are reported in Figure 5. It can be seen that, while the slopes pertaining to the sub-chance regime (i.e., $\alpha \ll .5$) are symmetrically distributed around zero, the distributions of the slopes pertaining to the chance regime ($\alpha \simeq .5$) are skewed towards negative values, as predicted in the above qualitative depiction of the two cases.

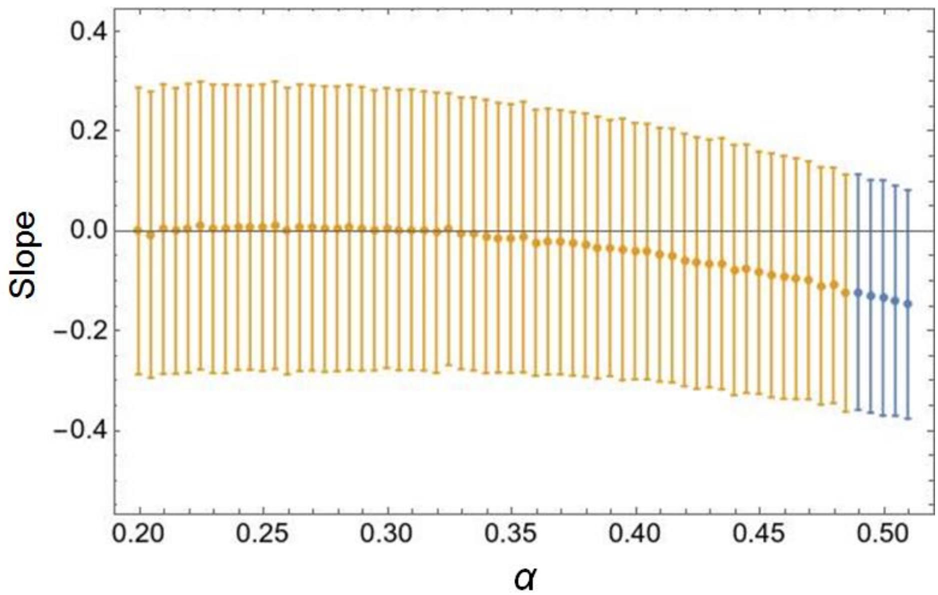

Figure 5. Distribution of the slopes associated to the late drifts of the simulated staircases as a function of the lower asymptote value, ranging from α = .2 (strongly sub-chance) to α = .51 (slightly above chance). The transition from the randomness of directions for $\alpha \ll .5$ (bright markers) to the negative skewness for $\alpha \simeq .5$ (dark markers) is apparent. Error bars ±SD.

Since the psychometric functions describing the responses of the actual participants are unknown, one cannot expect a full match between the simulation and the experimental data. However, from a qualitative point of view, the feature is undeniable, and it is theoretically justified by the introductory considerations. Therefore, an equivalent analysis was performed on the distributions of the slopes associated with the late drifts of the staircases of Experiment 1. Mean values and standard deviations of slopes for each GP type and each adapting condition are reported in Figure 6. The slopes are consistently skewed towards negative values, thus inconsistent with the hypothesis that the responses of the participants may be systematically lower than chance at low coherence levels.

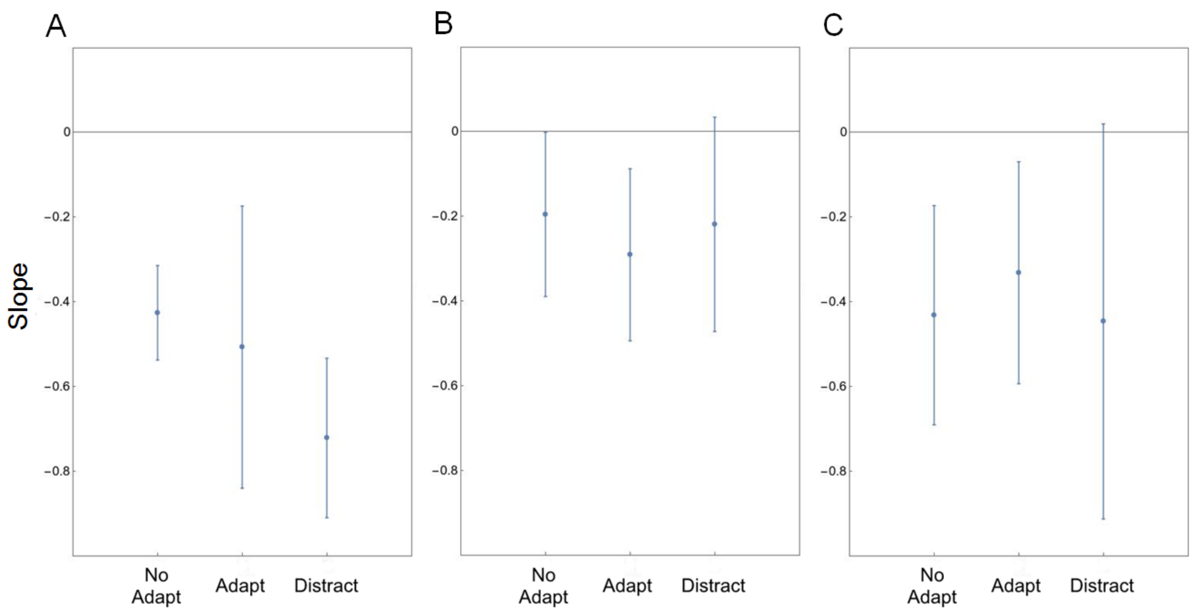

Figure 6. Distributions of the slopes associated to the late drifts of the staircases of Experiment 1, for translational (A), circular (B), and radial GPs (C). Error bars ±SD.

Discussion

The results of Experiment 1 showed that diverting attention away from the adapting pattern strengthens the adaptation to static structures, producing higher PSR values than in the non-distracted condition. In Experiment 2, we investigated the role of the attentional load using a low-load secondary task. The rationale was that a low-load attentional task should not affect the strength of adaptation, therefore we did not expect any effect of distraction.

Experiment 2

In Experiment 2 we used only vertical translational GPs. This choice was motivated by the following reasons: (i) an uncorrected post-hoc analysis on PSR values reported a significant difference between the non-distracted and distracted conditions only for translational GPs $t(8) = 2.34$, $p = .047$ (circular GPs: $t(8) = 1.79$, $p = .11$; radial GPs: $t(8) = 1.59$, $p = .15$), (ii) for translational GPs we found the largest difference between PSR values in the distracted and non-distracted conditions (translational GPs mean difference: .0884, SEM: .0377; circular GPs mean difference: .0627, SEM: .035; radial GP mean difference: .0734, SEM: .0461), (iii) there is evidence that when translational GPs are presented within a circular window, coherence thresholds are generally higher than those for circular GPs (Dakin, 1999; Wilson & Wilkinson, 1998; Wilson et al., 1997), a result also confirmed in our Experiment 1. However, Dakin and Bex (2002) proposed that the difference observed may be a result of the shape of the stimulus window. The authors found that when circular GPs were displayed in a square window, the lower detection threshold usually found in circular GPs was eliminated, being similar to those of translational GPs presented in a square window. The authors proposed that the circular shape of the window may add further global form cues facilitating spatial summation in rotational GPs. Therefore, when translational GPs are presented in a circular window less spatial summation is expected, consequently this configuration is particularly useful to test whether distraction is effective in reducing spatial suppression when using large field patterns.

Methods

Stimuli and Procedure

One of the authors (AP) and a different group of seven naïve participants took part voluntarily to the experiment. Stimuli and procedure were the same as in Experiment 1 except that we included an additional low-load attentional task during adaptation to translational GPs. The same observers performed both low- and high-load attentional conditions. In the low-load attentional condition letters and digits always composed the visual stream, but the presentation rate of digits over letters was 1/12. This presentation rate was established with a pilot experiment in order to establish a correct digit identification rate equal or higher to .95 (indicative of low load; see Motoyoshi et al., 2015). In this experiment, two participants (AP and AP2) performed three staircases instead of two in the no-adaptation condition. The PSR values were then averaged to get the final estimate of the PSR for the no-adaptation condition.

Results

Figure 7 shows the results of Experiment 2. A repeated measures ANOVA on PSR values reported a significant effect of the adapting condition (i.e., no-adaptation, non-distracted, high and low attentional load) $F(2, 21) = 27.15$, $p = .0001$, $\eta_p^2 = .795$. Post-hoc comparisons with FDR at .05 revealed a significant difference between the no-adapted condition and all the other adapting conditions (*adjusted-p* < .0001), between the non-distracted condition and the high-load attentional condition (*adjusted-p* = .0024), and between the non-distracted condition and the low-load attentional condition (*adjusted-p* =

.0015). However, post-hoc comparisons did not report a significant difference between the two attentional loads (*adjusted-p* = .9).

In Figure 7B, individual PSR values estimated in the non-distracted and distracted conditions are reported as a function of the PSR values for the no-adaptation condition. The majority of the points fall above the diagonal line indicating higher PSR for the adapting conditions (i.e., non-distracted, high- and low-load attentional conditions). Only 1 point out of 24 fall below the diagonal line indicating higher PSR in the no-adaptation condition than in the non-distracted adaptation condition.

As in Experiment 1, an analysis performed on the distributions of the slopes associated to the late drifts of the staircases showed that the slopes were consistently skewed towards negative values, thus suggesting that participants' responses were not systematically lower than chance at low coherence levels (slope no-adaptation condition: -.36, SD: .21; slope non-distracted condition: -.46, SD: .21; slope distracted high-load condition: -.52, SD: .18; slope distracted low-load condition: -.45, SD: .39).

The proportion of correctly identified digits in the high-load attentional task was .877 (SEM = .0159), whereas the proportion of correctly identified digits in the low-load attentional task was .955 (SEM = .0125) $t(7) = 6.66$, $p = .0001$. Additionally, the proportion of correctly identified digits in the low-load attentional condition did not significantly differ from .95, $t(7) = .42$, $p = .68$.

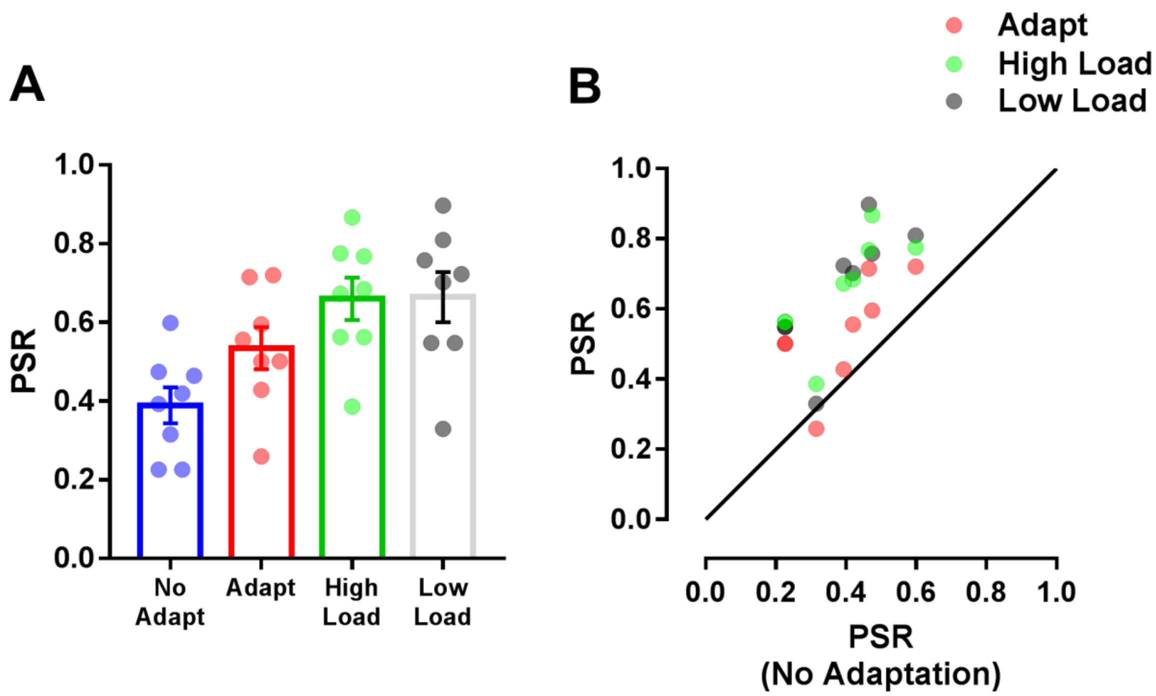

Figure 7. Results of Experiment 2. (A) Mean and individual PSR values for the adapting condition (i.e., no-adaptation, non-distracted, distracted high-load and distracted low-load). (B) Individual PSR values estimated in the non-distracted and distracted high- and low-load conditions as a function of PSR values estimated in the no-adaptation condition. The diagonal line indicates equal PSR values for the adaptation and no-adaptation conditions. Error bars ±SEM.

Discussion

The results of Experiment 2 replicated those of Experiment 1 and showed that diverting attention away from the adapting GP strengthened the adaptation, increasing the form after-effect. This counterintuitive result is compatible with recent findings of Motoyoshi and colleagues (2015) who found that distraction improves observers' performance in a global motion detection task. Motoyoshi et al. (2015) found that global motion detection is improved only when the attentional load of the secondary task is relatively low, though we did not find an effect of the attentional load.

Control Experiment on the effect of the attentional load on form adaptation

In Experiment 2 we found that the low-load attentional condition increased form adaptation as much as the high-load condition. Conventionally, in order to demonstrate that the high-load task requires more attentional resources, it is shown that accuracy is lower than in the low-load condition (Morgan, 2013; Rees, Frith, & Lavie, 1997). However, accuracy in the distracting secondary task does not tell us about the attentional resources allocated. In fact, participants could have devoted equal attentional resources to the secondary tasks and still allocated residual attentional resources to the adapting pattern (Morgan, 2013). In this control experiment we aimed to investigate whether participants attend less in the distracting conditions, and whether they attend less in the high-load task than in the low-load task.

We tested this by using a procedure similar to that employed by Morgan (2013). Two of the authors (AP and FG) and four naïve participants took part in the control experiment. The stimuli were vertical translational static GPs identical to those used in Experiments 1 and 2. GPs were presented for 10 s (corresponding to the top-up adaptation phase of Experiments 1 and 2). Participants had to detect a brief (.024 s) contrast decrement of the GP. The magnitude of the contrast decrement was regulated by a 1-up / 2-down staircase (Levitt, 1971). The contrast decrement could appear randomly at any time during the GP presentation and was presented on 75% of the trials. The staircase always terminated after 52 trials. This number of trials was chosen because in Experiment 2 the mean number of trials performed by the participants in both attentional conditions was 51.4 (SD = 19.7). At the beginning of the staircase the contrast of the GP was decreased from .99 to .8 during the brief contrast decrement. The contrast decrement was then decreased (i.e., towards .99) following two correct detection responses. The maximum contrast of the decrement could be .99. The initial step size of the staircase was .05, and it was halved after each reversal until a minimum step size of .006. The rationale was that if the distracting tasks use attentional resources, we should expect that observers can detect lower contrast decrements in the no-load condition than in the distracting conditions; that is, the contrast decrement threshold should be closer to .99 for the no-load condition than in the distracting conditions.

The contrast decrement threshold, corresponding to 70.7% correct detection, was calculated by averaging the GP contrast decrement levels presented by the staircase across all the 39 trials. Participants performed three conditions: a no-load condition, in which participants had only to detect the brief contrast decrement, a high-load and a low-load attentional condition, in which participants had to respond to the digits presented in the visual stream during the 10 s presentation of the translational GP, and at the end of the trial report whether there was or not a contrast decrement. The presentation rates of digits over letters were the same as used in Experiment 2; 1/3 and 1/12 for high- and low-load, respectively. Conditions were randomized across observers.

The contrast decrement thresholds were: .853 (SEM = .013) for the no-load condition, .8206 (SEM = .0166) for the high-load condition and .8279 (SEM = .0168) for the low-load condition. A repeated measures ANOVA conducted on the contrast decrement thresholds, showed a significant effect of the condition $F(2, 10) = 10.23$, $p = .004$, $\eta_p^2 = .67$. Post-hoc comparisons with FDR at .05 reported a significant difference between the no-load condition and the high-load condition (*adjusted-p* = .0255) and a significant difference between the no-load condition and the low-load condition (*adjusted-p* = .021), but no significant difference between the two distracting conditions (*adjusted-p* = .351). The false alarm rate was zero across all the conditions tested, indicating that participants never reported a contrast decrement when it was not presented. The results showed that in the no-load condition the observers could detect a lower contrast decrement than in the high- and low-load attentional conditions. The magnitude of the contrast decrement in the different attentional load conditions can be calculated by subtracting the contrast decrement threshold from .99. For the no-load condition the contrast decrement was .137, for the high-load condition was .1694 and for the low-load condition was .1621.

This suggests that the attentional tasks divert the attention of participants away from the adapting pattern, though some attentional resources can still be allocated to the adapting GP. Most importantly, we did not find any significant difference between the two attentional tasks, suggesting that the low-load task we used requires approximately the same attentional resources of the high-load task. This could explain why in Experiment 2 we did not find a significant difference between the two load conditions. Though the contrast decrement thresholds were similar in the two attentional tasks, the proportion of correctly identified digits in the high-load condition, .914 (SEM = .019), was significantly different from the proportion of correctly identified digits in the low-load condition, .95 (SEM = .011), $t(5) = -3.13$, $p = .026$. This clearly demonstrates that though accuracy varies significantly across the two attentional load conditions, the effect on attentional resources is approximately the same (Morgan, 2013).

Additionally, the proportion of correctly identified digits in the high-load attentional condition did not differ significantly from that of Experiment 2 in the same condition, $t(12) = 1.601$, $p = .135$. The same applies to the low-load attentional condition, $t(12) = -.40$, $p = .695$.

Experiment 3

Motoyoshi et al. (2015) suggested that limited attention might expand the spatial extent of signal integration by reducing suppression at high-levels of visual processing. In a series of additional experiments, we tested the role of spatial suppression in limiting the strength of form adaptation from translational GPs. Tadin and colleagues (2003), using a motion direction discrimination task, found that at high contrast (92%), the direction discrimination of a drifting Gabor patch was impaired (higher duration threshold) with increasing the stimulus size (up to 5 deg) and also reduced in its effectiveness as an adaptation stimulus. The authors interpreted this result as an effect of centre-surround antagonism at the level of individual neurons (i.e., surround suppression; Glasser & Tadin, 2011; Tadin & Lappin, 2005; Tadin et al., 2003). However, when using low contrast Gabors (2%) the authors found lower duration thresholds with increasing stimulus size, suggesting a shift from surround suppression to spatial summation (Tadin et al., 2003).

In Experiment 3, we measured the effect of distraction under two stimulus manipulations (A and B): (i) 3A - High-contrast GPs as in Experiments 1 and 2, but with a reduced size of the translational GPs. The rationale was that if distraction facilitates the spatial summation of oriented dipoles by weakening the suppression induced by large field GPs, then reducing the size of the GPs should reduce the amount of suppression, therefore we should not expect any effect of distraction; (ii) 3B - A stimulus size as large as those used in Experiments 1 and 2, but with lower dipole contrast. The rationale was that at low dipole contrast, higher sensitivity is necessary to extract the global form; therefore, lowering the stimulus contrast should promote spatial summation, cancelling out any effect of distraction.

Methods

Stimuli and Procedure

In Experiment 3A, one of the authors (AP) and a group of eight naïve participants took part in the experiment. The procedure was the same as in the previous experiments. However, we used smaller static translational GPs with high contrast dipoles (dot Weber contrast .99). The outer radius of the GP was 2.4 deg and the inner radius was .8 deg. In Experiment 3A, we used 198 dipoles to achieve the same dipole density as the previous experiments (i.e., 12.3 dipoles/deg^2). For Experiment 3A, two participants (CD, MP) performed three staircases for the no-adaptation condition, whereas one participant (RD) performed four staircases in the no-adaptation condition. Participant CD also performed two staircases in the distracted condition. In these cases the final PSR value was calculated by averaging the PSR values from each staircase.

In Experiment 3B, one of the authors (AP) and a different group of seven naïve participants took part in the experiment. In this experiment, GPs were the same as in Experiments 1 and 2 (static translational GPs with 2000 dipoles, radius 7.25 deg, density 12.3 dipoles/deg^2), but dot Weber contrast was .59. The same contrast was used for both adapting and test GPs. In Experiment 3B, for six participants out of eight only one staircase for the no-adaptation condition was considered (AB, AP, MK, RA, RC, and SW). This is because these participants exhibited higher PSR values in the no-adaptation condition than in the non-distracted condition over several repetitions of the no-adaptation condition. Therefore, for each participant we considered the no-adaptation condition showing lower PSR than the non-distracted condition.

In both experiments, participants performed no-adaptation, non-distracted and distracted conditions. In the distracted condition observers performed the high-load attentional task (i.e., digit-letter ratio of 1/3).

Results

Experiment 3A

Figure 8A shows the main results of Experiment 3A. A repeated measures ANOVA on PSR values reported a significant effect of the adapting condition (i.e., no-adaptation, non-distracted and distracted conditions) $F(2, 16) = 6.519$, $p = .008$, $\eta_p^2 = .449$. Post-hoc comparisons with FDR at .05 revealed a significant difference between the no-adapted condition and the non-distracted condition (*adjusted-p* = .009), and between the non-distracted and distracted conditions (*adjusted-p* = .033). However, post-hoc comparisons did not report a significant difference between the no-adapted and distracted conditions (*adjusted-p* = .347), suggesting that for small GPs, distraction affected the strength of adaptation and form after-effect.

In Figure 8B, individual PSR values estimated in the non-distracted and distracted conditions are reported as a function of the PSR values for the no-adaptation condition. For the non-distracted condition, the majority of the points fall above the diagonal line indicating higher PSR values. However, for the distracted condition 2 points out of 9 fall below the diagonal line indicating higher PSR in the no-adaptation condition. It should be noted that 5 points of the distracted condition are also very close to the equity line, suggesting similar PSR values between the no-adaptation and distracted conditions.

As in the previous experiments, an analysis performed on the distributions of the slopes associated to the late drifts of the staircases showed that the slopes were consistently skewed towards negative values, thus inconsistent with the hypothesis that the responses of the participants may be systematically lower than chance at low coherence levels (slope no-adaptation condition: -.35, SD: .17; slope non-distracted condition: -.32, SD: .22; slope distracted condition: -.39, SD: .25).

In order to test for differences between large and small GPs, we also performed a mixed ANOVA on PSR values including as between-subjects factor the GP size (large vs. small); PSR values for the large GP condition were taken from Experiment 2. For the distraction condition we considered the high-load distraction condition of Experiment 2. Given that author ‘AP’ participated in both experiments 2 and 3A, their data were removed from this analysis. As within-subjects factor we included the adaptation condition (i.e., non-distracted vs. distracted). In the analysis we included the no-adaptation condition as covariate. This model assesses the difference between PSR values in the non-distracted and distracted conditions for large and small GPs after accounting for the PSR values in the no-adaptation condition. The adjustment for the no-adaptation condition makes sure that any difference between the non-distracted and distracted conditions for the two GP sizes, truly result from the introduction of the distracting task, and are not some left-over effect of (random) baseline differences between the two GP sizes. Additionally, the model also accounts for variation of the adapting conditions that comes from the initial variation in the no-adaptation condition. Based on Schneider et al. (2015), when the expected value of a covariate measure is the same for each grouping of participants (in this case the GP size), one can use an ANCOVA provided that the covariate is centred before the analysis. Centering of the covariate is performed by subtracting the covariate mean from each score of the covariate across groups (i.e., GP size). An independent t-test did not report a significant difference between large and small GPs for the no-adaptation condition, $t_{13} = .109$, $p = .915$. Before performing the mixed ANCOVA, we checked for the assumptions. Assumptions were checked after centering the covariate (i.e., no-adaptation condition). The Levene's test of equality of variance showed that the error variance of the non-distracted and distracted conditions was equal across GP sizes, $p > .05$. The Box's test of equality of covariance matrices showed that the observed covariance matrices of the dependent variables were equal across GP sizes $p = .693$. The dependent variables (i.e., no-adaptation, non-distracted and distracted conditions) for each GP size were normally distributed $p > .05$. Additionally, the assumption of homogeneity of regression slopes was also met, which means that there was no interaction between the covariate and the independent variable (i.e., GP size) $F(1, 11) = .235$, $p = .637$, $\eta_p^2 = .021$, suggesting that the covariate can be introduced into the model. Figure 8C shows the comparison between non-distracted and distracted conditions for large and small GPs. The mixed ANOVA reported a significant interaction between adapting condition and GP size $F(1, 12) = 16.103$, $p = .002$, $\eta_p^2 = .573$. GP size and adaptation condition effects were not significant (GP size: $F(1, 12) = 2.72$, $p = .125$, $\eta_p^2 = .185$; adaptation condition: F(1,

12) = .076, p = .787, η_p^2 = .006). The ANOVA also reported a significant effect of the covariate $F(1, 12) = 9.394$, p = .01, η_p^2 = .439, suggesting that the no-adaptation condition explains a significant amount of variance in the adapting conditions. Post-hoc comparisons for the adapting condition x GP size interaction using FDR at .05, reported a significant difference between large and small GPs for the distracted condition (*adjusted-p* = .022). Post-hoc comparisons also pointed out a significant difference between non-distracted and distracted conditions for both large (*adjusted-p* = .018) and small GPs (*adjusted-p* = .018) (Figure 8C). These results confirmed that, after controlling for the no-adaptation condition (i.e., baseline), distraction has a detrimental effect on the strength of form adaptation when using small GPs. The proportion of correctly identified digits in the high-load attentional task was .87 (SEM = .021).

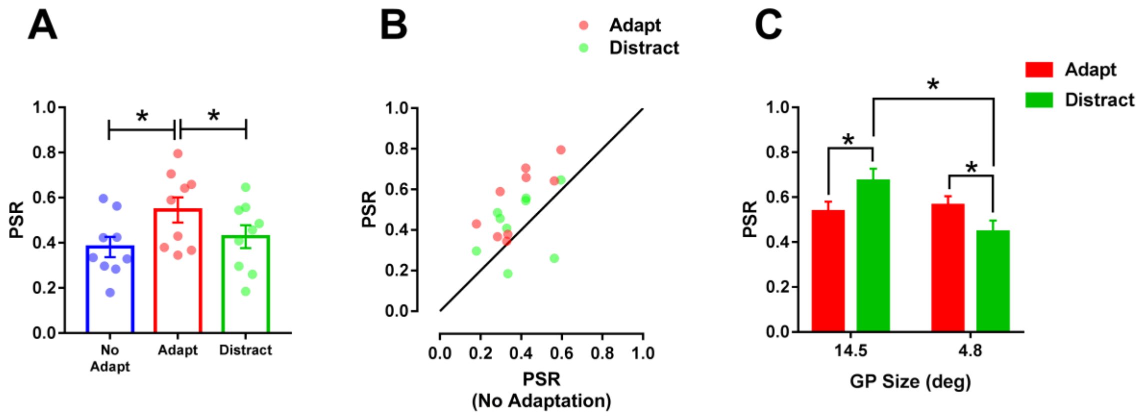

Figure 8. Results of Experiment 3A. (A) Mean and individual PSR values for the different adapting conditions (i.e., no-adaptation, non-distracted and distracted). (B) Individual PSR values estimated in the non-distracted and distracted conditions as a function of PSR values estimated in the no-adaptation condition. The diagonal line indicates equal PSR values for the adaptation and no-adaptation conditions. (C) Mean PSR values estimated in the non-distracted and distracted conditions after adjustment for the no-adaptation condition, for large (14.5 deg) and small (4.8 deg) GPs. Error bars ±SEM.

Experiment 3B

Figure 9A shows the results of Experiment 3B in which we manipulated dipoles contrast. A repeated measures ANOVA on PSR values reported a significant effect of the adapting condition (i.e., no-adaptation, non-distracted and distracted conditions) $F(2, 14) = 8.644$, $p = .004$, $\eta_p^2 = .553$. Post-hoc comparisons with FDR at .05 revealed a significant difference between the no-adapted and the non-distracted conditions (*adjusted-p* = .009) and between the no-adapted and the distracted conditions (*adjusted-p* = .045), but not a significant difference between the non-distracted and distracted conditions (*adjusted-p* = .19).

In Figure 9B, individual PSR values estimated in the non-distracted and distracted conditions are reported as a function of the PSR values for the no-adaptation condition. For the non-distracted condition, all the points but one fall above the diagonal line indicating higher PSR values for the non-distracted condition. However, for the distracted condition 3 points out of 8 fall below or on the diagonal line indicating either higher or equal PSR to the no-adaptation condition.

As in the previous experiments, an analysis performed on the distributions of the slopes associated to the late drifts of the staircases showed that the slopes were consistently skewed towards negative values, thus suggesting that participants' responses were not systematically lower than chance at low coherence levels (slope no-adaptation condition: -.39, SD: .27; slope non-distracted condition: -.50, SD: .25; slope distracted condition: -.45, SD: .26).

In order to test for differences between GPs with high and low dipoles contrast, we performed a mixed ANOVA on PSR values including as between-subjects factor the contrast of dipoles (high vs. low), with PSR values for the high-contrast condition from Experiment 2. Given that author 'AP' participated in both experiments 2 and 3B, their data were removed from the analysis. As within-subjects factor we included the adaptation condition (i.e., non-distracted vs. distracted). The no-adaptation condition was included as covariate. An independent t-test did not report a significant difference between high- and low-contrast for the no-adaptation condition (t_{12} = .504, p = .623). Before performing the mixed ANCOVA, we checked for the assumptions. The covariate was centred before assumptions checking. The Levene's test of equality of variance showed that the error variance of the non-distracted and distracted conditions was equal across contrast levels, $p > .05$. The Box's test of equality of covariance matrices showed that the observed covariance matrices of the dependent variables were equal across contrast levels p = .873. The dependent variables (i.e., no-adaptation, non-distracted and distracted conditions) for each contrast level were normally distributed $p > .05$. The assumption of homogeneity of regression slopes was also met, i.e., there was no interaction between the covariate and the independent variable GP contrast $F(1, 10) = 1.267$, p = .287, η_p^2 = .112.

Figure 9C shows the comparison between non-distracted and distracted conditions for high- and low-contrast GPs. The mixed ANOVA reported a significant interaction between adapting condition and GP contrast $F(1, 11) = 9.265$, p = .011, η_p^2 = .457. GP contrast and adaptation condition effects were not significant (GP contrast: $F(1, 11) = 1.006$, p = .337, η_p^2 = .084; adaptation condition $F(1, 11) = 2.756$, p = .125, η_p^2 = .2). The ANOVA also reported a significant effect of the covariate $F(1, 11) = 17.086$, p = .002, η_p^2 = .608, suggesting that the covariate explains a significant amount of variance in the dependent variables. Post-hoc comparisons for the adapting condition x GP contrast interaction using FDR at .05, reported only a significant difference between the non-distracted and distracted conditions for high-contrast GPs (*adjusted*-p = .014). These results suggest that, after controlling for the baseline, reducing the contrast of the GP cancelled out the effect of distraction on the strength of form adaptation. The proportion of correctly identified digits in the high-load attentional task was

.88 (SEM = .025) and did not significantly differ from the accuracy in the attentional task of Experiment 3A $t(15) = .56$, $p = .581$.

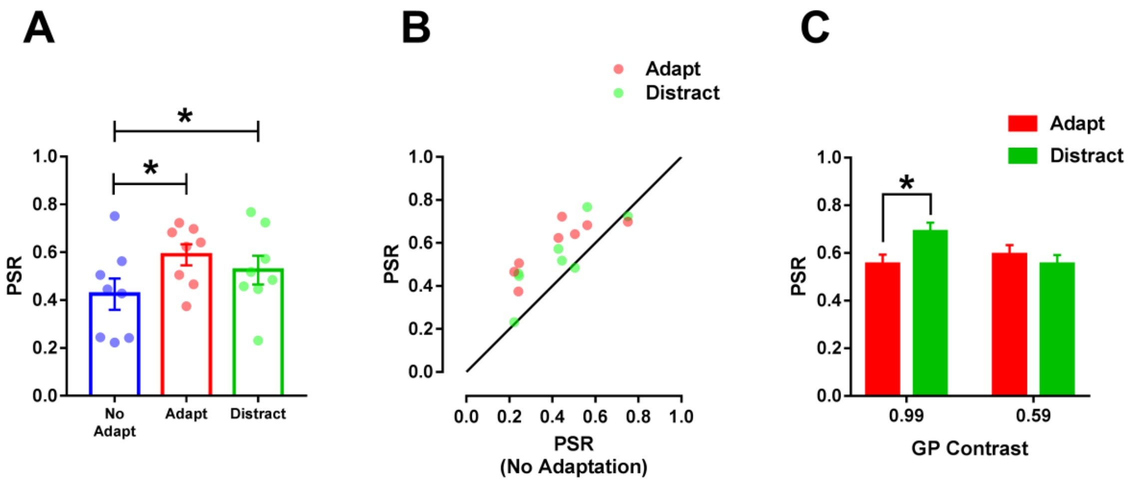

Figure 9. Results of Experiment 3B. (A) Mean and individual PSR values for the different adapting conditions. (B) Individual PSR values estimated in the non-distracted and distracted conditions as a function of PSR values estimated in the no-adaptation condition. (C) Mean PSR values estimated in the non-distracted and distracted conditions after adjustment for the no-adaptation condition for high- (.99) and low-contrast (.59) dipoles. Error bars ±SEM.

Discussion

The results of Experiment 3 showed that when reducing the size of GPs, distraction significantly reduced the strength of adaptation with respect to the non-distracted condition. On the other hand, lowering the contrast of both adapting and test GPs cancelled out the effect of distraction on the strength of adaptation and form after-effect. These results are compatible with a distraction-induced reduction of suppression of neurons responding to global form (Glasser & Tadin, 2011; Li & Chen, 2011; Liu, Haefner, & Pack, 2016; Tadin & Lappin, 2005; Tadin et al., 2003).

Experiment 4

In two additional experiments, we manipulated different spatial parameters of the GPs. In particular, we assessed whether decreasing the adapter density (Experiment 4A) and coherence (Experiment 4B) also reduced the amount of suppression, thus decreasing (or cancelling out) the effect of distraction.

Methods

Stimuli and Procedure

A different sample of eleven naïve participants took part to the density experiment (Experiment 4A), and one of the authors (FG) and six naïve participants took part to the coherence experiment (Experiment 4B). The procedure was the same as in the previous experiments. The GPs had a size of 14.5 deg and participants always performed a high-load secondary attentional task during adaptation.

In Experiment 4A we used static translational GPs with a density four times lower than that used in previous experiments (3.07 dipoles/deg^2). In Experiment 4B, observers were adapted to static translational GPs with a coherence of 70%.

Results

Experiment 4A

Figure 10A shows the results of Experiment 4A in which we used a lower dipole density. A repeated measures ANOVA on PSR values reported a significant effect of the adapting condition $F(2, 20) = 13.088$, $p = .0001$, $\eta_p^2 = .567$. Post-hoc comparisons with FDR at .05 revealed a significant difference between the no-adapted condition and the non-distracted (*adjusted-p* = .0001) and distracted conditions (*adjusted-p* = .036), but not a significant difference between the non-distracted and distracted conditions (*adjusted-p* = .056).

In Figure 10B, individual PSR values estimated in the non-distracted and distracted conditions are reported as a function of the PSR values for the no-adaptation condition. For the non-distracted condition, all the points fall above the diagonal line indicating overall higher PSR values for the non-distracted condition. However, for the distracted condition 4 points out of 11 fall below the diagonal line indicating higher PSR for the no-adaptation condition.

An analysis performed on the distributions of the slopes associated to the late drifts of the staircases showed that the slopes were consistently skewed towards negative values, thus inconsistent with the hypothesis that participants' responses were systematically lower than chance at low coherence levels (slope no-adaptation condition: -.36, SD: .15; slope non-distracted condition: -.33, SD: .31; slope distracted condition: -.45, SD: .23).

In order to test for differences between GPs with high and low density, we performed a mixed ANCOVA on PSR values including as between-subjects factor the dipole density, with PSR values for the high density condition from Experiment 2. The data of one participant (DW) were excluded from the present analysis because they participated in both experiments 2 and 4A. As within-subjects factor we included the adaptation condition (i.e., non-distracted vs. distracted). The no-adaptation condition was included as covariate. An independent t-test did not report a significant difference between high and low density GPs for the no-adaptation condition (t_{15} = .172, p = .866). Before performing the mixed ANCOVA, we checked for the assumptions. The covariate was centred before assumptions checking. The Levene's test of equality of variance showed that the error variance of the non-distracted and distracted conditions was equal across dipoles density levels $p > .05$. The Box's test of equality of covariance matrices showed that the observed covariance matrices of the dependent variables were equal across density levels p = .295. The dependent variables (i.e., no-adaptation, non-distracted and distracted conditions) for each density level were normally distributed $p > .05$. Additionally, the assumption of homogeneity of regression slopes was also met, i.e., there was no interaction between the covariate and the independent variable GP density $F(1, 13) = .03$, $p = .865$, $\eta_p^2 = .002$.

Figure 10C shows the comparison between non-distracted and distracted conditions for high and low density GPs. The mixed ANOVA reported a significant interaction between adapting condition and GP density $F(1, 14) = 11$, $p = .005$, $\eta_p^2 = .44$. GP density and adaptation condition effects were not significant (GP density: $F(1, 14) = .061$, $p = .808$, $\eta_p^2 = .004$; adaptation condition: $F(1, 14) = .074$, $p = .789$, $\eta_p^2 = .005$). The ANOVA also reported a significant effect of the covariate $F(1, 14) = 33.55$, $p = .0001$, $\eta_p^2 = .706$, suggesting that the covariate explains a significant amount of variance in the dependent variable. Post-hoc comparisons for the adapting condition x GP density interaction using FDR at .05, reported a significant difference between the non-distracted and distracted conditions for both high and low density GPs (*adjusted-p* = 0.035). These results suggest that, after controlling for the baseline, distraction has a detrimental effect on form adaptation when using low density GPs.

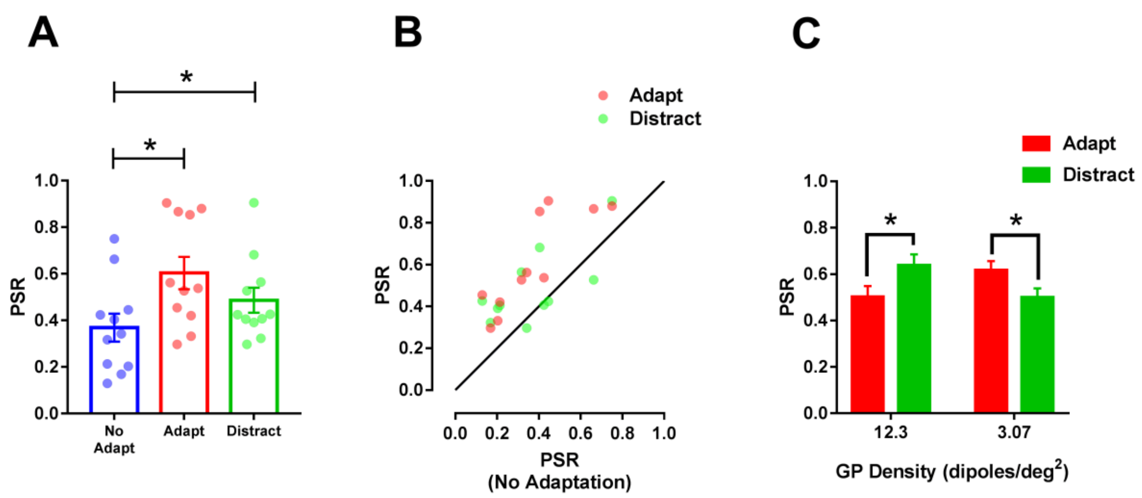

Figure 10. Results of Experiment 4A. (A) Mean and individual PSR values for the different adapting conditions. (B) Individual PSR values estimated in the non-distracted and distracted conditions as a function of PSR values estimated in the no-adaptation condition. (C) Mean PSR values estimated in the non-distracted and distracted conditions after adjustment for the no-adaptation condition for high and low density dipoles. Error bars ±SEM.

Experiment 4B

Figure 11A shows the results of Experiment 4B in which we used a lower coherence of the adapting GP. A repeated measures ANOVA on PSR values reported a significant effect of the adapting condition $F(2, 16) = 7.926$, $p = .004$, $\eta_p^2 = .498$. Post-hoc comparisons with FDR at .05 revealed a significant difference between the no-adapted condition and the non-distracted condition (*adjusted-p* = .003), but not a significant difference between the no-adapted condition and the distracted condition (*adjusted-p* = .0825) and between the non-distracted and distracted conditions (*adjusted-p* = .262).

In Figure 11B, individual PSR values estimated in the non-distracted and distracted conditions are reported as a function of the PSR values for the no-adaptation condition. For the non-distracted condition, all the points fall above the diagonal line indicating higher PSR values for the non-distracted condition. However, for the distracted condition 2 points out of 9 fall below the diagonal line indicating higher PSR for the no-adaptation condition, and 1 point fall on the line, indicating a similar PSR value for the no-adapted and distracted conditions.

As in the previous experiments, an analysis performed on the distributions of the slopes associated to the late drifts of the staircases showed that the slopes were consistently skewed towards negative values, thus inconsistent with the hypothesis that the responses of the participants may be systematically lower than chance at low coherence levels (slope no-adaptation condition: -.52, SD: .15; slope non-distracted condition: -.43, SD: .38; slope distracted condition: -.51, SD: .30).

In order to test for differences between high and low adapting coherence, we performed a mixed ANOVA on PSR values including as between-subjects factor the adapting coherence (100% vs. 70%). PSR values for the high adapting coherence condition were taken from Experiment 2. As within-subjects factor we included the adaptation condition (i.e., non-distracted vs. distracted). The no-adaptation condition was included as covariate. An independent t-test did not report a significant difference between high and low adapting coherence levels for the no-adaptation condition (t_{15} = .725, p = .480). Before performing the mixed ANCOVA, we checked for the assumptions. The covariate was centred before assumptions checking. The Levene's test of equality of variance showed that the error variance of the non-distracted and distracted conditions was equal across adapting coherence levels, $p > .05$. The Box's test of equality of covariance matrices showed that the observed covariance matrices of the dependent variables were equal across adapting coherence levels $p > .05$. The dependent variables (i.e., no-adaptation, non-distracted and distracted conditions) for each coherence level were normally distributed $p > .05$. Additionally, the assumption of homogeneity of regression slopes was also met, i.e., there was no interaction between the covariate and the independent variable adapting GP coherence $F(1, 13) = .957$, $p = .346$, $\eta_p^2 = .069$.

Figure 11C shows the comparison between non-distracted and distracted conditions for high- and low-coherence adapting GPs. The mixed ANOVA with the no-adaptation condition as covariate reported only a significant interaction between adapting condition and adapting GP coherence $F(1, 14) = 9.192$, $p = .009$, $\eta_p^2 = .396$. GP coherence and adaptation condition effects were not significant (GP coherence: $F(1, 14) = .514$, $p = .485$, $\eta_p^2 = .035$; adaptation condition: $F(1, 14) = .692$, $p = .419$, $\eta_p^2 = .047$). The ANOVA also reported a significant effect of the covariate $F(1, 14) = 5.694$, $p = .032$, $\eta_p^2 = .289$, suggesting that the covariate explains a significant amount of variance in the dependent variables. Post-hoc comparisons for the adapting condition x adapting GP coherence interaction using FDR at .05, only reported a significant difference between non-distracted and distracted conditions for the high coherence adaptation (*adjusted-p* = 0.036). These results suggest that, after controlling for the baseline, reducing the coherence of the adapting GPs, cancelled out the effect of distraction on the strength of form adaptation.

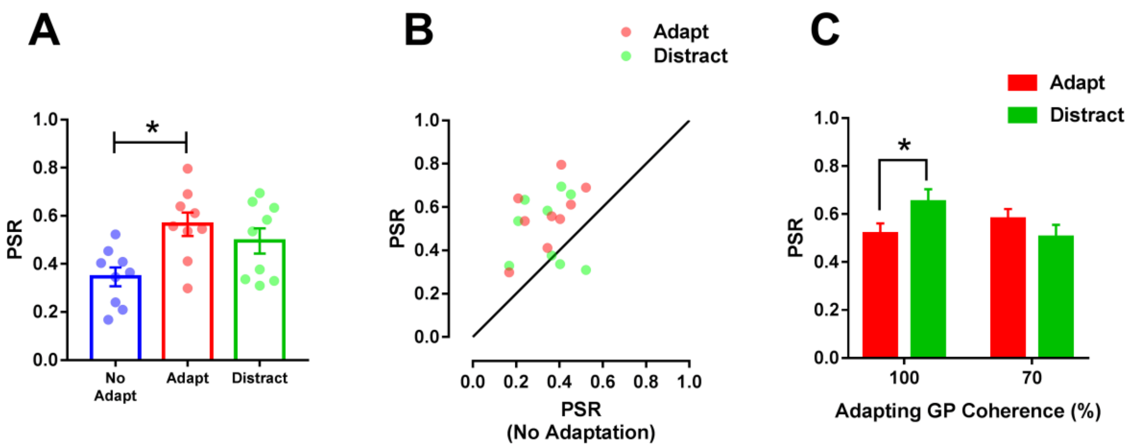

Figure 11. Results of Experiment 4B. (A) Mean and individual PSR values for the different adapting conditions. (B) Individual PSR values estimated in the non-distracted and distracted conditions as a function of PSR values estimated in the no-adaptation condition. (C) Mean PSR values estimated in the non-distracted and distracted conditions after adjustment for the no-adaptation condition for high- and low-density dipoles. Error bars ±SEM.

Discussion

The results of Experiment 4 resemble those of Experiment 3, showing that the effect of distraction is detrimental on form adaptation and form after-effect when using low density GPs. On the other hand, the effect of distraction is cancelled out when using low coherence adapting GPs, with no evident difference between the non-distracted and distracted conditions. These results confirm that the manipulations have the effect of decreasing the spatial suppression induced by large field GPs. Besides, the results show that distraction is no longer effective in strengthening form adaptation, suggesting its involvement in the modulation of spatial suppression.

Experiment 5

In Experiment 5 observers were adapted and tested with dynamic GPs (Ross, Badcock, & Hayes, 2000). There is psychophysical evidence that dynamic GPs show lower detection and coherence thresholds than static GPs (Nankoo et al., 2015; Pavan et al., 2017), suggesting the involvement of a temporal summation mechanism in addition to spatial summation (Nankoo et al., 2015). The rationale was to investigate distraction effects also exist for dynamic GPs. Distraction effects may not be evident with dynamic GPs because of the additional temporal summation that could prevent or limit spatial suppression.

Methods

Stimuli and Procedure

A new sample of nine naïve participants took part to Experiment 5. The procedure was the same as that used in the previous experiments. The spatial parameters of dynamic GPs were the same as those for static GPs in Experiment 1 (12.3 dipoles/deg^2, dot width of .04 deg, inter-dot spacing of .18 deg, Weber contrast of each dot .99, diameter of the outer annulus 14.5 deg). We employed a high-load attentional task during adaptation.

Dynamic GPs were obtained by sequentially displaying a series of stationary GPs at a rate of 21.3 Hz (frame duration ~ .046 ms). This temporal frequency was chosen since Nankoo et al. (2015) found lower detection thresholds for 20 Hz dynamic translational GPs. For each frame, a new GP was created by randomizing the spatial location of the dipoles but keeping the same local orientation. The sequential presentation of different static translational GPs produces the impression of motion along the orientation axis, though it is not directional (Nankoo, Madan, Spetch, & Wylie, 2012; Ross, 2004; Ross et al., 2000). During the adapting phase, dynamic GPs were presented at 100% coherence, and at maximum contrast (.99 Weber contrast).

Results

Figure 12A shows the main results of Experiment 5. A repeated measures ANOVA on PSR values reported a significant effect of the adapting condition $F(2, 16) = 26.49$, $p = .0001$, $\eta_p^2 = .768$. Post-hoc comparisons with FDR at .05 revealed a significant difference between the no-adapted condition and the non-distracted condition (*adjusted-p* = .0015), and between the no-adapted and distracted conditions (*adjusted-p* = .0003). However, post-hoc comparisons did not report a significant difference between the non-distracted and distracted conditions (*adjusted-p* = .478), suggesting that for dynamic GPs, distraction did not affect the strength of adaptation and form after-effect.

In Figure 12B, individual PSR values estimated in the non-distracted and distracted conditions are reported as a function of the PSR values for the no-adaptation condition. All of the points but one fall above the diagonal line indicating higher PSR values for the adapting conditions.

An analysis performed on the distributions of the slopes associated to the late drifts of the staircases showed that the slopes were consistently skewed towards negative values, with exception of the distracted condition. In this particular case the symmetry of the distribution of the slopes around zero could indicate that the PSR is not an asymptotic value, but an actual point of the psychometric function (see the results section of Experiment 1 for more details) (slope no-adaptation condition: -.16, SD: .18; slope non-distracted condition: -.25, SD: .28; slope distracted condition: -.03, SD: .30).

In order to test for differences between dynamic and static GPs, we performed a mixed ANOVA on PSR values including as between-subjects factor the GP type (static vs. dynamic); PSR values for the static GP type were taken from Experiment 2. As within-subjects factor we included the adaptation condition (i.e., non-distracted vs. distracted). The no-adaptation condition was included as covariate. An independent t-test reported a significant difference between static and dynamic GPs for the no-adaptation condition (t_{15} = 4.134, p = .001). Based on Schneider et al. (2015) when the covariate measures in the two groups (i.e., static vs. dynamic GPs) are significantly different, conducting an ANCOVA can lead to errors, and they recommend a different approach. The recommended procedure is to conduct a standard ANCOVA to test the hypotheses concerning the effect of covariate and the within-subjects factor x covariate interaction, and to use a standard repeated measures ANOVA (i.e., without the covariate) to evaluate all the other effects. Before performing the ANCOVA, we checked for the assumptions. The covariate was centred before assumptions checking. The Levene's test of equality of variance showed that the error variance of the non-distracted and distracted conditions was equal across GP types (i.e., static and dynamic), $p > .05$. The Box's test of equality of covariance matrices showed that the observed covariance matrices of the dependent variables were equal across GP types, $p > .05$. The dependent variables (i.e., non-distracted and distracted conditions) for each GP type were normally distributed $p > .05$. Additionally, the assumption of homogeneity of regression slopes was also met, which means that there was no interaction between the covariate and the independent variable (i.e., GP type) $F(1, 13) = .683$, $p = .424$, $\eta_p^2 = .05$. In this hybrid analysis, the only test taken from the within-subjects section of the ANCOVA is the adaptation condition x no-adaptation (i.e., covariate) interaction, which was not significant

$F(1, 14) = 1.522$, $p = .238$, $\eta_p^2 = .098$, and the only test taken from the between-subjects section of the ANCOVA was the main effect of the covariate (i.e., no-adaptation condition), which was significant $F(1, 14) = 9.506$, $p = .008$, $\eta_p^2 = .404$, again suggesting that the covariate explains a significant amount of variance in the dependent variable. The tests of the main effect due to the within factor (i.e., adaptation condition and interaction between adaptation condition and GP type) were taken from the within-subjects section of the standard repeated measures ANOVA, and the main effect of the GP type was taken from the between-subjects section of the standard ANOVA. The standard repeated measures ANOVA reported a significant effect of the adapting condition $F(1, 15) = 8.378$, $p = .011$, $\eta_p^2 = .358$, but not a significant interaction between adaptation condition and GP type $F(1, 15) = 2.939$, $p = .107$, $\eta_p^2 = .164$. The main effect of the GP type was significant $F(1, 15) = 9.565$, $p = .0087$ $\eta_p^2 = .389$. Though the interaction adaptation condition x GP type was not significant, post-hoc comparisons with FDR at .05 ,showed a significant difference between static and dynamic GPs for the distracted condition (*adjusted-p* = .004), and a significant difference between the non-distracted and distracted conditions for static GPs (*adjusted-p* = 0.012).

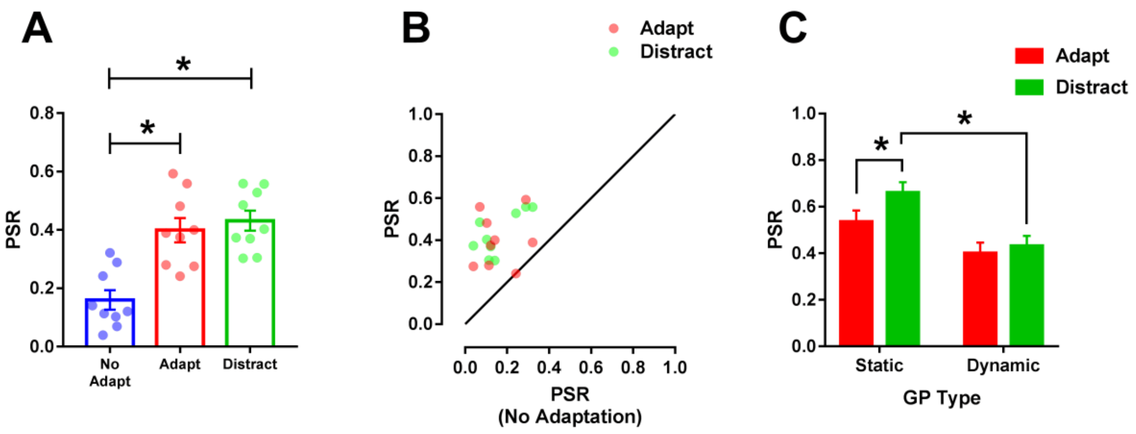

Figure 12. Results of Experiment 5. (A) Mean and individual PSR values for the different adapting conditions (i.e., no-adaptation, non-distracted and distracted). (B) Individual PSR values estimated in the non-distracted and distracted conditions as a function of PSR values

estimated in the no-adaptation condition. The diagonal line indicates equal PSR values for the adapted and no-adapted conditions. (C) Mean PSR values estimated in the non-distracted and distracted conditions after adjustment for the no-adaptation condition for static and dynamic GPs. Data for static GPs were gathered from Experiment 2. Error bars ±SEM.

Discussion

Overall, the results of Experiment 5 showed that form adaptation from dynamic GPs with an optimal temporal frequency for detection, was not modulated by distraction. In particular, we did not find any significant increment or decrement of the form after-effect following adaptation to dynamic GPs in the distracted condition. It is worth noting that the symmetric distribution of late drift slopes reported in the distracted condition could be a hint of a systematic sub-chance bias for low coherence levels. However, a single positive result over a large number of trials (i.e., over seven experiments of three conditions each, and four conditions in the case of Experiment 2) could be a statistical artefact.

General Discussion

In a series of experiments, we investigated whether the spatial summation of local oriented cues (dipoles) in Glass patterns (GPs) depends on visuospatial attention. The study was motivated by brain imaging evidence that visuospatial attention enhances information processing and integration at early levels of processing (Cohen & Tong, 2015; Haynes et al., 2005; Jehee et al., 2011; Ling et al., 2015; Liu et al., 2007; McAdams & Maunsell, 1999a, 1999b; Motter, 1993; Poltoratski et al., 2017; Pratte et al., 2013; Somers et al., 1999; Treue & Martinez-Trujillo, 2007). In the first experiment, we used large-scale GPs (14.5 deg in diameter) of different configurations (i.e., translational, circular and radial) and assessed the role of attention in spatial summation of local dipoles by using a form adaptation paradigm

(Clifford & Weston, 2005; Pavan et al., 2016; Vreven & Berge, 2007) and a secondary task during adaptation to divert the attention away from the adapting pattern (Kaunitz et al., 2011; Morgan, 2011, 2012, 2013; Pavan & Greenlee, 2015). In particular, in the non-distracted adaptation condition observers were adapted to coherent GPs. After the adaptation period, they were presented with a test GP divided in two halves along the vertical. One side of the test GP was completely random (i.e., with randomly oriented dipoles), whereas the other side was more coherent. Observers were required to judge which side of the test GP was more coherent. In the attention-distracted adaptation condition, a rapid serial visual presentation task was performed during the adapting period. The magnitude of the form after-effect from GP adaptation was expressed in terms of the change in the point of subjective randomness (PSR) tracked by 1-up / 1-down staircases (Levitt, 1971). The PSR was defined as the coherence level of the test GP for which observers were at chance in discriminating the most coherent side. The rationale was that if visuospatial attention has a modulatory effect on the spatial summation of local orientation signals to extract global form, then diverting the attention away from the adapting GP should strongly reduce the form after-effect. A dedicated analysis of the behaviour of the late drift of the staircases provided an almost complete confutation of the hypothesis of systematic sub-chance responses at low coherence levels.

The results of Experiment 1 showed that diverting the attention away from the adapting GP had the effect of strengthening the adaptation and increasing the consequent form after-effect. In fact, form adaptation with a concomitant high-load secondary task had the effect of increasing PSR values. We argue that enhanced adaptation due to a secondary task during the adapting period is due to a reduction in spatial suppression. In a series of additional experiments, we found that the beneficial effects of limiting attention *decrease or vanish* when specific spatial and temporal properties of the adapting GPs are manipulated.

This was evident even after adjusting for the no-adaptation condition. In Experiment 3 we manipulated the size and the contrast of the adapting GPs; if a reduction in spatial suppression from large-scale stimuli is involved in the attentional effects we reported, then decreasing the size of the adapting GP but using high contrast dipoles, should decrease the spatial suppression, whereas decreasing the contrast of the dipoles but adapting to a large field GP should induce a stronger spatial summation, thus dramatically decreasing the effect of distraction during adaptation (Tadin et al., 2003). The results of Experiment 3 showed that these two manipulations effectively reduced the effect of distraction, supporting the notion that suppression may be involved in the processing of large-scale stationary textures. In Tadin et al. (2003), the maximum spatial suppression was found when using a stimulus size of 5 deg; a size that well approximates the dimension of foveal MT center-surround receptive fields in macaque monkeys (Raiguel, Van Hulle, Xiao, Marcar, & Orban, 1995). Additionally, it has been demonstrated that the optimal stimulus size decreases with increasing contrast. For example, Tadin and Lappin (2005) found that at high contrast (92%) sensitivity for motion direction is higher when the Gabor patch is less than 1 deg (see Tadin, 2015). However, in our case the lack of an effect of distraction during adaptation (compatible with reduced suppression) was found with GPs having a diameter of 4.8 deg (Experiment 3A). This points to differences in patterns of spatial suppression between neurons responding to global form and motion. It is possible that in the case of global form perception, suppression is more evident when using large-scale textures (Dickinson et al., 2009), pointing to the involvement of neurons with large receptive fields in the extraction of global form from GPs. There is brain imaging evidence that translational as well as complex GPs are analysed by striate and extrastriate areas (e.g., V2, V3, V3A, VP/V3, hV4 and LOC) (Ostwald et al., 2008). Mannion et al. (2010) also reported sensitivity to curvature and global form across many early visual areas, including V1, V2, V3 and hV4. Therefore, high level visual areas may be involved not only in the extraction of global form but also in the regulation of spatial suppression. In fact, there is neurophysiological and computational evidence that feedback connections from higher level visual areas not only improve form and shape selectivity of high level neurons (Jehee, Roelfsema, Deco, Murre, & Lamme, 2007), but also contribute to surround suppression at low levels of visual analysis (Nassi, Lomber, & Born, 2013; Sullivan & de Sa, 2006). For example, Nassi et al. (2013) showed that, for large gratings stimulating regions beyond the center of the receptive field, inactivation of feedback from areas V2 and V3 of macaque monkeys resulted in strong and consistent response facilitation, effectively reducing the strength of surround suppression in V1 for stimuli of both low and high contrast.

Though these results show that low and high level visual areas contribute to the extraction of global form and feedback connections from high level areas contributes to spatial suppression at the level of the striate cortex, they do not explain how distraction can reduce spatial suppression from large-scale visual stimuli. Our additional spatial manipulations on the adapter density (Experiment 4A) and coherence (Experiment 4B) had the effect of abolishing the effect of distraction, possibly by reducing the amount of suppression; that is, once the amount of spatial suppression (as measured in the non-distracted conditions) is reduced distraction is no longer effective.

Overall, consistent results had been previously reported in the motion domain by Motoyoshi et al. (2015). These authors showed that limited attention increases coherence sensitivity in a motion direction discrimination task when the size of the random dot kinematograms (RDKs) was large (7.9 and 16 deg), when the dot density was high (up to 400 dots), when contrast was high (.80), and when the speed was higher than 1.2 deg/s. Though form and motion discrimination are not equivalent, our findings and those of Motoyoshi et al.

(2015) support the notion of a distraction-related reduction of suppression and increased spatial integration of local signals, at least under the conditions tested.

How can limiting attention reduce the spatial suppression from large-field static textures? Liu et al. (2016) recorded the activity of small populations of neurons in the MT areas of two macaque monkeys. Monkeys were trained to report the direction of a drifting grating changing in size on a trial by trial basis. Consistent with previous findings (Tadin & Lappin, 2005; Tadin et al., 2003), the authors reported that increasing stimulus size led to an impairment of monkeys' behavioural performance. Cell population recordings revealed that the magnitude of the neuronal surround suppression exhibited by individual neurons was too small to account for the behavioural findings. However, additional analysis of population recordings and computational modelling revealed that neural noise correlations (i.e., correlation of the fluctuations in responses to the same stimulus among nearby neurons; Cohen & Kohn, 2011) further suppressed the population coding for large stimuli. As reported by Ecker et al. (2011) neurons with similar stimulus selectivity will exhibit higher noise correlations than others. Therefore, in a homogeneous neural population (i.e., in neurons that receive the same external input and in which interaction strength is assumed to be uniform), this limited range correlation structure highly affects the accuracy of the population code. In fact, decorrelated neural activity after adaptation or after perceptual learning corresponds to a more efficient population coding (Benucci, Saleem, & Carandini, 2013; Ecker et al., 2011; Gu et al., 2011; Gutnisky & Dragoi, 2008; Haak, Fast, Baek, & Mesik, 2014). In our case, distraction during adaptation may have further contributed in reducing noise correlations amongst neurons with similar orientation selectivity, thus promoting spatial integration and resulting in a stronger after-effect.

A further finding is that for dynamic GPs there is no effect of distraction during adaptation (Experiment 5). Based on the previous explanation it is possible that for dynamic

GPs the fast update of the spatial arrangement of oriented dipoles reduces noise correlations amongst units responding to these local oriented cues. Consistently, there is psychophysical evidence of weak surround suppression for flicker-defined form stimuli, and this surround suppression is independent from surround size (Denniss & Mckendrick, 2016).

In general, the underlying mechanisms of distraction-related reduced suppression and the role of high level areas in this process are not clear, and more psychophysical, neuroimaging and cell recording studies are necessary to understand this phenomenon.

Acknowledgements

This study was supported by the University of Lincoln. We thank Rita Donato for help in data collection.

Data availability

Raw data are available from the corresponding author upon request.

References

Anderson, S. J., & Burr, D. C. (1991). Spatial summation properties of directionally selective mechanisms in human vision. *Journal of the Optical Society of America. A, Optics and Image Science*, *8*(8), 1330–1339. http://doi.org/10.1364/JOSAA.8.001330

Benucci, A., Saleem, A. B., & Carandini, M. (2013). Adaptation maintains population homeostasis in primary visual cortex. *Nature Neuroscience*, *16*(6), 724–729. http://doi.org/10.1038/nn.3382

Born, R. T., Groh, J. M., Zhao, R., & Lukasewycz, S. J. (2000). Segregation of object and background motion in visual area MT: effects of microstimulation on eye movements. *Neuron*, *26*, 725–734. http://doi.org/10.1016/S0896-6273(00)81208-8

Braddick, O. (1993). Segmentation versus integration in visual motion processing. *Trends in Neurosciences*, *16*(7), 263-268. http://doi.org/10.1016/0166-2236(93)90179-P

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436. http://doi.org/10.1163/156856897X00357

Chung, C. Y. L., & Khuu, S. K. (2014). The processing of coherent global form and motion patterns without visual awareness. *Frontiers in Psychology*, *5*, 195. http://doi.org/10.3389/fpsyg.2014.00195

Churan, J., Khawaja, F. A., Tsui, J. M. G., & Pack, C. C. (2008). Brief motion stimuli preferentially activate surround-suppressed neurons in macaque visual area MT. *Current Biology*, *18*(22), R1051-2. http://doi.org/10.1016/j.cub.2008.10.003

Clifford, C. W. G., & Weston, E. (2005). Aftereffect of adaptation to Glass patterns. *Vision Research*, *45*(11), 1355–1363. http://doi.org/10.1016/j.visres.2004.12.016

Cohen, E. H., & Tong, F. (2015). Neural Mechanisms of Object-Based Attention. *Cerebral Cortex*, *25*(4), 1080–1092. http://doi.org/10.1093/cercor/bht303

Cohen, M. R., & Kohn, A. (2011). Measuring and interpreting neuronal correlations. *Nature Neuroscience*, *14*(7), 811-819. http://doi.org/10.1038/nn.2842

Dakin, S. C. (1997). The detection of structure in glass patterns: Psychophysics and computational models. *Vision Research*, *37*(16), 2227–2246. http://doi.org/10.1016/S0042-6989(97)00038-2

Dakin, S. C. (1999). Orientation variance as a quantifier of structure in texture. *Spatial Vision*, *12*, 1–30. http://dx.doi.org/10.1163/156856899X00012

Dakin, S. C., & Bex, P. J. (2001). Local and global visual grouping: Tuning for spatial frequency and contrast. *Journal of Vision*, *1*(2), 99–111. http://doi.org/Artn 4\rDoi 10.1167/1.2.4

Dakin, S. C., & Bex, P. J. (2002). Summation of concentric orientation structure: Seeing the

Glass or the window? *Vision Research*, *42*(16), 2013–2020. http://doi.org/10.1016/S0042-6989(02)00057-3

Denniss, J., & Mckendrick, A. M. (2016). Flicker-defined form stimuli are minimally affected by centre-surround lateral contrast interactions. *Ophthalmic and Physiological Optics*, *36*(2), 174–182. http://doi.org/10.1111/opo.12268

Dickinson, J. E., Broderick, C., & Badcock, D. R. (2009). Selective attention contributes to global processing in vision. *Journal of Vision*, *9*(2), 6.1-8. http://doi.org/10.1167/9.2.6

Ecker, A. S., Berens, P., Tolias, A. S., & Bethge, M. (2011). The Effect of Noise Correlations in Populations of Diversely Tuned Neurons. *Journal of Neuroscience, 31*(40), 14272–14283. http://doi.org/10.1523/JNEUROSCI.2539-11.2011

Glass, L. (1969). Moiré Effect from Random Dots. *Nature*, *223*, 578–580. http://doi.org/10.1038/223578a0

Glass, L., & Pérez, R. (1973). Perception of random dot interference patterns. *Nature, 246*(5432), 360-362. https://doi:10.1038/246360a0

Glass, L., & Switkes, E. (1976). Pattern recognition in humans: correlations which cannot be perceived. *Perception, 5*(1), 67-72. https://doi.org/10.1068/p050067

Glasser, D. M., & Tadin, D. (2011). Increasing stimulus size impairs first- but not second-order motion perception. *Journal of Vision, 11*(13), 1–8. http://doi.org/10.1167/11.13.22

Gu, Y., Liu, S., Fetsch, C. R., Yang, Y., Fok, S., Sunkara, A., DeAngelis, G. C., & Angelaki, D. E. (2011). Perceptual learning reduces interneuronal correlations in macaque visual cortex. *Neuron*, *71*(4), 750–761. http://doi.org/10.1016/j.neuron.2011.06.015

Gutnisky, D. A., & Dragoi, V. (2008). Adaptive coding of visual information in neural populations. *Nature*, *452*(7184), 220–224. http://doi.org/10.1038/nature06563

Haak, K. V, Fast, E., Baek, Y., & Mesik, J. (2014). Equalization and decorrelation in primary visual cortex. *Journal of Neurophysiology, 112*(3), 501-503.

http://doi.org/10.1152/jn.00521.2013

Haynes, J.-D., Tregellas, J., & Rees, G. (2005). Attentional integration between anatomically distinct stimulus representations in early visual cortex. *Proceedings of the National Academy of Sciences*, *102*(41), 14925–14930. http://doi.org/10.1073/pnas.0501684102

Jehee, J. F. M., Brady, D. K., & Tong, F. (2011). Attention improves encoding of task relevant features in the human visual cortex. *Journal of Neuroscience*, *31*(22), 8210–8219. http://doi.org/10.1523/JNEUROSCI.6153-09.2011

Jehee, J. F. M., Roelfsema, P. R., Deco, G., Murre, J. M. J., & Lamme, V. A. F. (2007). Interactions between higher and lower visual areas improve shape selectivity of higher level neurons-Explaining crowding phenomena. *Brain Research*, *1157*(1), 167–176. http://doi.org/10.1016/j.brainres.2007.03.090

Kaunitz, L., Fracasso, A., & Melcher, D. (2011). Unseen complex motion is modulated by attention and generates a visible aftereffect. *Journal of Vision*, *11*(13), 10. http://doi.org/10.1167/11.13.10

Levitt, H. (1971). Transformed Up-Down Methods in Psychoacoustics. *The Journal of the Acoustical Society of America*, *49*(2), Suppl 2:467+. http://doi.org/10.1121/1.1912375

Li, H. H., & Chen, C. C. (2011). Surround modulation of global form perception. *Journal of Vision*, *11*(1), 17. http://doi.org/10.1167/11.1.17

Ling, S., Pratte, M. S., & Tong, F. (2015). Attention alters orientation processing in the human lateral geniculate nucleus. *Nature Neuroscience*, *18*(4), 496–498. http://doi.org/10.1038/nn.3967

Liu, L. D., Haefner, R. M., & Pack, C. C. (2016). A neural basis for the spatial suppression of visual motion perception. *eLife*, *5*, e16167. http://doi.org/10.7554/eLife.16167

Liu, T., Larsson, J., & Carrasco, M. (2007). Feature-Based Attention Modulates Orientation-Selective Responses in Human Visual Cortex. *Neuron*, *55*(2), 313–323.

http://doi.org/10.1016/j.neuron.2007.06.030

Mannion, D. J., McDonald, J. S., & Clifford, C. W. G. (2009). Discrimination of the local orientation structure of spiral Glass patterns early in human visual cortex. *NeuroImage*, *46*(2), 511–515. http://doi.org/10.1016/j.neuroimage.2009.01.052

Mannion, D. J., McDonald, J. S., & Clifford, C. W. G. (2010). The influence of global form on local orientation anisotropies in human visual cortex. *NeuroImage*, *52*(2), 600–605. http://doi.org/10.1016/j.neuroimage.2010.04.248

Maruya, K., Watanabe, H., & Watanabe, M. (2008). Adaptation to invisible motion results in low-level but not high-level aftereffects. *Journal of Vision*, *8*(11), 1–11. http://doi.org/10.1167/8.11.7.Introduction

McAdams, C. J., & Maunsell, J. H. (1999a). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *The Journal of Neuroscience*, *19*(1), 431–41.

McAdams, C. J., & Maunsell, J. H. (1999b). Effects of attention on the reliability of individual neurons in monkey visual cortex. *Neuron*, *23*(4), 765–773. http://doi.org/S0896-6273(01)80034-9

Morgan, M. J. (2011). Wohlgemuth was right: Distracting attention from the adapting stimulus does not decrease the motion after-effect. *Vision Research*, *51*(20), 2169–2175. http://doi.org/10.1016/j.visres.2011.07.018

Morgan, M. J. (2012). Motion adaptation does not depend on attention to the adaptor. *Vision Research*, *55*, 47–51. http://doi.org/10.1016/j.visres.2011.12.009

Morgan, M. J. (2013). Sustained attention is not necessary for velocity adaptation. *Journal of Vision*, *13*(8), 1–11. http://doi.org/10.1167/13.8.26

Morgan, M. J. (2014). A bias-free measure of retinotopic tilt adaptation. *Journal of Vision,* *14*(1): 7. doi: 10.1167/4.1.7

Motoyoshi, I., Ishii, T., & Kamachi, M. G. (2015). Limited attention facilitates coherent motion processing. *Journal of Vision*, *15*(13), 1. http://doi.org/10.1167/15.13.1

Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *Journal of Neurophysiology*, *70*(3), 909–919. http://doi.org/0022-3077/93

Nankoo, J. F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2012). Perception of dynamic Glass patterns. *Vision Research*, *72*, 55–62. http://doi.org/10.1016/j.visres.2012.09.008

Nankoo, J. F., Madan, C. R., Spetch, M. L., & Wylie, D. R. (2015). Temporal summation of global form signals in dynamic Glass patterns. Vision Research, 107, 30-35. doi: 10.1016/j.visres.2014.10.033

Nassi, J. J., Lomber, S. G., & Born, R. T. (2013). Corticocortical Feedback Contributes to Surround Suppression in V1 of the Alert Primate. *Journal of Neuroscience*, *33*(19), 8504–8517. http://doi.org/10.1523/JNEUROSCI.5124-12.2013

Ostwald, D., Lam, J. M., Li, S., & Kourtzi, Z. (2008). Neural coding of global form in the human visual cortex. *Journal of Neurophysiology*, *99*(5), 2456–2469. http://doi.org/10.1152/jn.01307.2007

Pack, C. C. (2004). Contrast Dependence of Suppressive Influences in Cortical Area MT of Alert Macaque. *Journal of Neurophysiology*, *93*(3), 1809–1815. http://doi.org/10.1152/jn.00629.2004

Palomares, M., Ales, J. M., Wade, A. R., Cottereau, B. R., & Norcia, A. M. (2012). Distinct effects of attention on the neural responses to form and motion processing: A SSVEP source-imaging study. *Journal of Vision*, *12*(10), 15–15. http://doi.org/10.1167/12.10.15

Pavan, A., Ghin, F., Donato, R., Campana, G., & Mather, G. (2017). The neural basis of form and form-motion integration from static and dynamic translational Glass patterns: A rTMS investigation. Neuroimage, 157, 555-560. doi: 10.1016/j.neuroimage.2017.06.036

Pavan, A., & Greenlee, M. W. (2015). Effects of crowding and attention on high-levels of motion processing and motion adaptation. *PLoS ONE*, *10*(1). http://doi.org/10.1371/journal.pone.0117233

Pavan, A., Hocketstaller, J., Contillo, A., & Greenlee, M. W. (2016). Tilt aftereffect following adaptation to translational Glass patterns. *Scientific Reports*, *6*, 23567. http://doi.org/10.1038/srep23567

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, *10*(4), 437–442. http://doi.org/10.1163/156856897X00366

Poltoratski, S., Ling, S., McCormack, D., & Tong, F. (2017). Characterizing the effects of feature salience and top-down attention in the early visual system. *Journal of Neurophysiology*, *118*(1), 564–573. http://doi.org/10.1152/jn.00924.2016

Price, N. S. C., & Prescott, D. L. (2012). Adaptation to direction statistics modulates perceptual discrimination. *Journal of Vision,* 12(6):32. doi: 10.1167/12.6.32

Pratte, M. S., Ling, S., Swisher, J. D., & Tong, F. (2013). How attention extracts objects from noise. *Journal of Neurophysiology*, *110*(6), 1346–1356. http://doi.org/10.1152/jn.00127.2013

Prins, N., & Kingdom, F. A. A. (2009). Palamedes: Matlab routines for analyzing psychophysical data. http://www.palamedestoolbox.org

Raiguel, S., Van Hulle, M. M., Xiao, D. -K, Marcar, V. L., & Orban, G. A. (1995). Shape and Spatial Distribution of Receptive Fields and Antagonistic Motion Surrounds in the Middle Temporal Area (V5) of the Macaque. *European Journal of Neuroscience*, *7*(10), 2064–2082. http://doi.org/10.1111/j.1460-9568.1995.tb00629.x

Rees, G., Frith, C. D., & Lavie, N. (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science*, *278*, 1619–1619.

Ross, J. (2004). The perceived direction and speed of global motion in Glass pattern sequences. *Vision Research, 44*(5), 441–448.

Ross, J., Badcock, D. R., & Hayes, A. (2000). Coherent global motion in the absence of coherent velocity signals. *Current Biology, 10*(11), 679–682. http://doi.org/10.1016/S0960-9822(00)00524-8

Ross, J., & Edwin Dickinson, J. (2007). Effects of adaptation to Glass pattern structure and to path of optic flow. *Vision Research*, *47*(16), 2150–2155. http://doi.org/10.1016/j.visres.2007.03.026

Ruff, D. A., & Cohen, M. R. (2016). Attention Increases Spike Count Correlations between Visual Cortical Areas. *Journal of Neuroscience*, *36*(28), 7523–7534. http://doi.org/10.1523/JNEUROSCI.0610-16.2016

Schneider, B. A., Avivi-Reich, M., & Mozuraitis, M. (2015). A cautionary note on the use of the Analysis of Covariance (ANCOVA) in classification designs with and without within-subject factors. *Frontiers in psychology*, *6*, 474. doi:10.3389/fpsyg.2015.00474

Smith, M. A., Bair, W., & Movshon, J. A. (2002). Signals in macaque striate cortical neurons that support the perception of glass patterns. *Journal of Neuroscience*, *22*(18), 8334–8345. http://doi.org/22/18/8334

Smith, M. A, Kohn, A., & Movshon, J. A. (2007). Glass pattern responses in macaque V2 neurons. *Journal of Vision*, *7*(3), 5. http://doi.org/10.1167/7.3.5

Snowden, R. J., & Milne, A. B. (1997). Phantom motion after effects-evidence of detectors for the analysis of optic flow. *Current Biology, 7*(10), 717-722. https://doi.org/10.1016/S0960-9822(06)00329-0

Somers, D. C., Dale, A. M., Seiffert, A. E., & Tootell, R. B. (1999). Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *96*(4), 1663–1668.

http://doi.org/10.1073/pnas.96.4.1663

Sullivan, T. J., & de Sa, V. R. (2006). A model of surround suppression through cortical feedback. *Neural Networks*, *19*(5), 564–572. http://doi.org/10.1016/j.neunet.2005.12.003

Swettenham, J. B., Anderson, S. J., & Thai, N. J. (2010). MEG responses to the perception of global structure within glass patterns. *PLoS ONE*, *5*(11). http://doi.org/10.1371/journal.pone.0013865

Tadin, D. (2015). Suppressive mechanisms in visual motion processing: From perception to intelligence. *Vision Research*, *115*, 58–70. http://doi.org/10.1016/j.visres.2015.08.005

Tadin, D., & Lappin, J. S. (2005). Optimal size for perceiving motion decreases with contrast. *Vision Research*, *45*(16), 2059–2064. http://doi.org/10.1016/j.visres.2005.01.029

Tadin, D., Lappin, J. S., Gilroy, L. a, & Blake, R. (2003). Perceptual consequences of centre – surround antagonism in visual motion processing. *Nature*, *424*(July), 312–315. http://doi.org/10.1038/nature01812.1.

Tadin, D., Paffen, C. L. E., Blake, R., & Lappin, J. S. (2008). Contextual modulations of center-surround interactions in motion revealed with the motion aftereffect. *Journal of Vision*, *8*, 9.1-11. http://doi.org/10.1167/8.7.9

Tadin, D., Silvanto, J., Pascual-Leone, A., & Battelli, L. (2011). Improved Motion Perception and Impaired Spatial Suppression following Disruption of Cortical Area MT/V5. *Journal of Neuroscience*, *31*(4), 1279–1283. http://doi.org/10.1523/JNEUROSCI.4121-10.2011

Treue, S., & Martinez-Trujillo, J. C. (2007). Attending to Features inside and outside the Spotlight of Attention. *Neuron*, 55(2), 174-176. http://doi.org/10.1016/j.neuron.2007.07.005

Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, *8*(8), 1096–1101. http://doi.org/10.1038/nn1500

Tsuchiya, N., Koch, C., Gilroy, L. a, & Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. *Journal of Vision*, *6*(10), 1068–78. http://doi.org/10.1167/6.10.6

Vreven, D., & Berge, J. (2007). Detecting structure in Glass patterns: An interocular transfer study. *Perception*, *36*(12), 1769–1778. http://doi.org/10.1068/p5777

Watson, A. B., & Turano, K. (1995). The optimal motion stimulus. *Vision Research*, *35*(3), 325–336. http://doi.org/10.1016/0042-6989(94)00182-L

Wilson, H. R., & Wilkinson, F. (1998). Detection of global structure in Glass patterns: Implications for form vision. *Vision Research*, *38*(19), 2933–2947. http://doi.org/10.1016/S0042-6989(98)00109-6

Wilson, H. R., Wilkinson, F., & Asaad, W. (1997). Concentric orientation summation in human form vision. *Vision Research*, *37*(17), 2325–2330. http://doi.org/10.1016/S0042-6989(97)00104-1

World Medical Association (2013). World Medical Association Declaration of Helsinki. Ethical principles for medical research involving human subjects. *Journal of the American Medical Association*, *310*, 2191–2194. https://www.wma.net/policies-post/wma-declaration-of-helsinki-ethical-principles-for-medical-research-involving-human-subjects/

Wright, M. J., & Johnston, A. (1985). Invariant tuning of motion aftereffect. *Vision Research,* *25*(12), 1947-1955. https://doi.org/10.1016/0042-6989(85)90019-7